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Cover Illustration: Massive clusters of monarch butterflies festoon the boughs of a cedar tree (*Cupressus lusitanica*) located in the Ojo de Agua arroyo that runs down the south facing slope of Cerro Pelon, one of the three major overwintering areas in the Monarch Butterfly Biosphere Reserve in the State of Mexico. Photo by L.P. Brower, 13 January 2006. (See article on page 177).



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MONARCH BUTTERFLY CLUSTERS PROVIDE MICROCLIMATIC ADVANTAGES DURING THE OVERWINTERING SEASON IN MEXICO

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ABSTRACT. Monarch butterflies form dense clusters in their overwintering colonies in the mountains of central Mexico, where forest cover provides protection from environmental extremes. We tested the hypothesis that the clustering behavior of the butterflies further moderates the microclimate they experience. We inserted hygrochrons (miniaturized digital hygrothermographs) into clusters for two-day periods during the 2006–07 and 2007–08 winters and compared temperature and relative humidity inside and outside the clusters. The inside of the clusters remained significantly warmer at night and significantly cooler during the day, with higher relative humidity during both day and night. Consequently, the butterflies inside the clusters may have gained some protection from freezing, reduced their rate of lipid burning, and lowered their rate of desiccation. The differences were small, but these studies were conducted during calm, moderate conditions, and the effects are likely to be more pronounced under more severe weather, including mid-winter storms and late season aridity. The microclimatic advantages of the monarchs' clustering behavior on fir boughs add to the known repertoire of the butterflies' overwintering adaptations to the high altitude environment that they occupy each year from November through March.

Additional key words: aggregation, insulation, clustering behavior, temperature, humidity.

Aggregation behavior is widespread in the animal kingdom and confers two major adaptive advantages to individuals: protection from predators and favorable modification of microclimate. Forming tight groups in many species of vertebrates and invertebrates reduces the probability, through the selfish herd effect, that any one individual will be killed (Hamilton 1971; Gamberale & Tullberg 1998). This advantage is enhanced when the

individuals are chemically defended (Brower 1984; Pough 1988; Sillen-Tullberg & Leimer 1988). The monarch butterfly (*Danaus plexippus* L., Lepidoptera, Danainae) is a classical example. The extreme densities of overwintering butterflies reduce the likelihood of any individual being attacked, as does their ability to store cardiac glycosides that are emetic to vertebrate predators (Brower *et al.* 1967; Brower 1984; Seiber *et*

al. 1986). These poisons reduce avian predation by reinforcing learned visual aversion of the butterflies' orange, black, and white warning coloration. Though substantial predation in the overwintering colonies in Mexico occurs by orioles and grosbeaks (Calvert *et al.* 1979; Fink & Brower 1981; Brower & Calvert 1985) and by certain species of mice (Brower *et al.* 1985), the majority of birds (Fink *et al.* 1983; Brower & Fink 1985) and mice (Glendinning & Brower 1990) are substantially deterred.

Microclimatic effects also influence aggregations, with animals often choosing sites where conditions are moderated. Numerous insects are known to respond to small differences in temperature and humidity (Cloudsley-Thompson 1962; Waldbauer 2000); for example, ladybird beetles and weevils aggregate where humidity is higher (Simpson & Welborn 1975), and cutworm moths aggregate in alpine talus (White *et al.* 1998), where temperatures are less extreme. Also, animals may create moderated conditions within their aggregations. For example, cockroaches and crickets generate higher humidity within their clusters (Dembach & Goehlen 1999; Yoder *et al.* 2002). Our study explored possible microclimatic advantages that

monarch butterflies derive from their clustering behavior.

One of the great biological spectacles on earth is the aggregation behavior of monarch butterflies at their overwintering sites in the Transverse Neovolcanic Range in central Mexico (Brower 1995). Arriving on at least twelve separate mountain massifs (Slayback *et al.* 2007; Slayback & Brower 2007) in early November, the butterflies form extremely dense clusters on the boughs and trunks of coniferous trees in colonies that, by mid-December, range in area from 0.01 to 6.14 hectares (Fig. 1). The largest combined area of monarch clusters occurred during the 1996–1997 overwintering season (Missrie 2004; Slayback *et al.* 2007), with an estimated combined total of 18 hectares of forest festooned with butterflies. Recent estimates indicate that there are at least 50 million butterflies per hectare (Brower *et al.* 2004), so that the 1996–1997 aggregations contained about 900 million monarchs.

Even though the overwintering area of monarch butterflies is south of the Tropic of Cancer, the 3000 m plus elevation of the mountains on which they form their colonies subjects them to freezing temperatures. Their greatest natural mortality occurs by freezing to



FIG. 1. Aerial photograph of the Piedra Herrada overwintering colony in an oyamel fir forest in the state of Mexico. In mid to late Dec 2006, this small colony occupied 0.27 ha (Rendon-Salinas *et al.* 2007). The butterflies likely avoid clustering in the tree tops in order to avoid freezing from exposure to the cold night sky. 13 Feb 2007.



FIG. 2. The density of clustering monarchs varies according to the foliage architecture of the tree species on which they settle. Note the exceedingly dense clusters on the oyamel fir (left foreground) and the much smaller ball-like clusters on the pine (right background). Photo taken in the Ojo de Agua ravine on Cerro Pelon in the state of Mexico, 13 Feb 2004.

death after northern rain and snowstorm incursions wet them, followed by plunging temperatures as the weather clears. One such storm in January 1981 was estimated to have killed more than 2.5 million monarchs in a Sierra Chincua colony (Calvert *et al.* 1983), and in January 2002 a major winter storm killed nearly half a billion monarchs across the overwintering region (Brower *et al.* 2004).

By forming their colonies in dense coniferous forests and by avoiding the tree tops, monarchs derive microclimatic protection from the forest canopy that acts as a blanket and reduces the rate of radiant heat loss to the sky (Calvert & Brower 1981). This blanket effect is dramatically demonstrated by large differences in both maximum and minimum daily temperatures inside the forest compared to nearby open areas (Brower & Calvert 1985). A second microclimatic advantage of the forest canopy is that it acts as a partial umbrella and helps to prevent the butterflies from getting wet during winter rain and snowstorms (Anderson & Brower 1996). These authors also discovered that overwintering monarchs can withstand freezing at body temperatures down to about -8°C , but their natural cryoprotection is substantially lost if their bodies become wet. When the forest is thinned, holes are punched in the blanket and umbrella, and both the thermal and sheltering advantages are diminished (Calvert *et al.* 1983).

Based on observations of the sites dating back to 1977, the three most utilized tree species are, in order of importance: the oyamel fir, *Abies religiosa* H. B. K. (Pinaceae), the smooth bark Mexican pine, *Pinus pseudostrobus* Lindl. (Pinaceae), and the Mexican cedar, *Cupressus lusitanica* Miller (Cupressaceae) (synonym of *C. lindleyi*; GRIN, 2007). The architectures of individual clusters are determined by the growth form of the boughs and needles of the tree species on which the butterflies settle (Figs. 2, 3A–C). Anderson & Brower (1996) found that butterflies inside fir clusters gain an important microclimatic advantage: they did not get as wet as those on the outside (Fig 4). The authors deduced that individuals within the clusters would more likely survive subfreezing temperatures.

This paper presents the results of field experiments begun in 2007 and repeated in 2008 designed to test the hypothesis that butterflies inside the clusters are insulated by those on the outside, with three possible microclimatic advantages. First, during lethal temperature drops, the butterflies inside may remain warmer. Second, during the day when temperatures climb, the inner butterflies may stay cooler, thereby preserving their lipid reserves. Lipids are critical both for winter survival (Masters *et al.* 1988) and for the surviving monarchs' spring remigration back to the Gulf

Coast (Malcolm *et al.* 1993). Third, the butterflies on the inside of a cluster may enjoy higher humidity, thus reducing evaporation and desiccation, which intensify as the dry season advances and millions of monarchs engage in long to-and-fro flights to drink water.

MATERIALS AND METHODS

Location of the study sites. The colonies studied in both years were located in the Sierra Chincua massif in Michoacan, Mexico. Their coordinates were determined using a Garmin-CS GPS unit and the Angangueo topographic map (INEGI 1999). On 8 January 2007, the position of the colony near its upper boundary was $100^{\circ} 17' 58''\text{W}$, $19^{\circ} 40' 31''\text{N}$, at an elevation of 3256 m. This is at the head of the western-most tributary leading down into the Arroyo Hondo. On 5 February 2008, the colony was located 1.1 km to the east of the 2007 site, slightly east of the eastern-most tributary of Arroyo Hondo, at approximately $100^{\circ} 17' 19''\text{W}$, $19^{\circ} 40' 06''\text{N}$, at an elevation of 3317 m. Both of these areas have hosted overwintering colonies in almost exactly the same positions as reported nearly 30 years ago and in numerous overwintering seasons since then (Calvert & Brower 1986; Missrie 2004).

Hourly temperature and humidity data on the same dates were recorded by an electronic weather station (WeatherHawk, Model 232, Logan, UT) located on the Monarch Butterfly Biosphere Reserve (MBBR) Field Station on El Llano las Papas ($100^{\circ} 16' 6.2''\text{W}$, $19^{\circ} 39' 41.9''\text{N}$, elevation 3160 m). The field station is on the eastern edge of the Sierra Chincua in an open llano (field) adjacent to an oyamel fir forest. It is approximately 3.6 km ESE of our 2007 experimental site, and approximately 2.5 km ESE of our 2008 site. The WeatherHawk recorded temperature each hour averaged over the previous hour. All data were downloaded into spreadsheets for analyses. A hygchron attached to the underside of the weather station provided a direct comparison to the measurements of the other hygchrons used in the experiment.

Temperature and humidity measurements of the clusters. For successive nights in both 2007 and 2008, we measured temperature and relative humidity inside and immediately outside monarch clusters that had assembled on the boughs of oyamel fir trees within the Chincua colony. The recording devices (Fig. 5) were iButton Hygchrons (model DS1923, Dallas Semiconductor Corporation), which are small electronic disks (1.59 cm by 0.64 cm). The hygchrons were set to record an instantaneous reading once every twenty minutes.

For 2008, the hygchrons were evaluated by



FIG. 3. (a) An early winter cluster of monarchs on an oyamel fir, likely the optimal tree species substrate for the butterflies to hold onto and form extremely dense, bag-like clusters having a large volume to surface area ratio. Photo taken in the Sierra Chincua colony in the state of Michoacan, 9 Dec 2006.

comparing their readings under identical conditions. All hygrochrons were placed in the same plastic bag to record temperature and humidity every 20 min during 13 hours of warm, room-temperature conditions (40 records) and 10 hours of cold, refrigerated conditions (30 records). We compared the average of the test readings for every pair of hygrochrons used in an inside-outside comparison across a cluster. When the average reading of one hygrochron under test conditions was less than the other, that difference was added to the measurements from the field of the first hygrochron. We applied adjustments to the field data separately for day measurements (adjustments from the warm readings) and night measurements (adjustments from



FIG. 3. (b) An early winter cluster on a cedar tree, which has flatter needles and is likely a less optimal substrate for dense clusters than the fir. Photo taken on the Llano de los Tres Gobernadores colony, on Cerro Pelon in the state of Mexico, 11 Dec 2006.

the refrigerated readings). These sensors are advertised as having an accuracy of $\pm 0.5^\circ\text{C}$ and a resolution of 0.6% RH. We did not compare their accuracy against known standards, but by our measurements, the hygrochrons gave such little variation in their readings that, in comparing them, we found the S.D. of the differences in temperature of each pair to range from only 0.03 to 0.07°C. That meant that each sensor gave highly consistent readings and that, with precision, paired hygrochrons could measure differences of less than 0.1°C. Relative humidity readings were more variable, with S.D. of all pairwise differences ranging from 0.58 to 0.97%.

Inserting the hygrochrons into the clusters.

Four (2007) or three (2008) hygrochrons were attached with ©Velcro to 89 cm long by 0.95 cm diameter wooden dowels at approximately 20 cm intervals. The end of a #18 twisted nylon twine leading off a spool was then attached with duct tape to the top of the hygrochron dowel. To lift the string that was attached to the hygrochron dowel, we used a 3 m extensible pole to which a second dowel with a bent hook nailed into its end was taped. We raised the pole so that the hygrochron dowel attached to the string hung directly over the cluster center. By gently playing out the string through the hook to avoid disturbing the cluster, the dowel was lowered into the cluster center. Once vertically positioned, we carefully twisted the pole to release the string from the hook and then secured the string to hold the dowel in place with at least one hygrochron inside and one outside the cluster (Fig. 5).

Experiments. The goal was to compare the temperature and relative humidity inside and immediately outside the monarch clusters. In 2007,



FIG. 3. (c) A late winter cluster on a pine tree, the least favorable of the three major coniferous substrates for dense clusters. The ball-like pine clusters are smaller than those that form on the firs and cedars, thus providing less microclimatic protection. Photo taken in the Ojo de Agua ravine, 9 Mar 2006.



FIG. 4. Monarchs clustering on oyamel fir branches wetted by an early December storm. The small silverish spots are water drops. Note that the fir boughs provide an umbrella effect and that there are few raindrops on the butterflies. This microclimatic effect is greater in larger clusters where the butterflies inside the cluster have less or no water on them. Photo taken in the Sierra Chincua Arroyo Hondo colony in the state of Michoacan, 9 Dec 2006.

preliminary studies were run on two clusters (A1, A2), while also positioning a single outside hygrochron on a dead oyamel tree branch less than 10 m away (A3). The dowels were in place from 1540 on 8 Jan 2007 to 0940 on 10 Jan 2007. We used binoculars to confirm that the dowels maintained their positions inside the clusters throughout the experiment.

We repeated the experiment in February 2008, placing dowels with sensors into six clusters (B1–B6). To obtain repeated ambient measures inside the colony, three control hygrochrons were attached to another dowel (B7) that we hung from an oyamel tree branch on the western edge of the colony at about the same height as the study clusters. Three dowels (B1–B3) were in place from 1700 on 5 Feb to 1530 on 7 Feb, and an additional three dowels (B4–B6) were in place from 1200 on 6 Feb to 1500 on 7 Feb. The data from one cluster (B2) were later deleted from the analysis because butterflies subsequently surrounded all the hygrochrons, so there was no inside-outside comparison. The five other dowels yielded readings for two days (10 day-time comparisons), while two dowels



FIG. 5. The experimental dowel inserted into experimental cluster 2 on an oyamel fir bough on 9 Jan 2007. The bottom of the dowel with an exposed hygrochron is evident; the other three hygrochrons are inside the cluster. The inset is a closeup of a hygrochron attached to a dowel with Velcro.

recorded for two nights and the other three for a single night (7 night-time comparisons).

The hygrochrons recorded temperature and relative humidity every 20 min, but for analysis, we standardized the times for comparison as day, 1200–1700, and night, 0000–0800. These were the times recorded by the ambient hygrochrons as being the warmest and coolest periods of a 24 hour day and thus the times when insulating of the clusters would be the most important.

We also recorded wind speed in the colony during the 2008 experiment with a Wind Speed Smart Sensor attached to a HOBO Micro Station (Onset Computer Corp.). This instrument yielded the average and maximum wind speed during each five-min time block from 1800 on 5 Feb 2008 to 1430 on 7 Feb 2008.

Description of the clusters. Qualitative observations indicated that there were fewer large clusters during both overwintering seasons than has been the case in the past, and they were less dense than in most previous years. Daytime temperatures were high enough that care was necessary not to disturb the butterflies and cause them to "explode" out of the clusters. Over the course of the 2007 experiment, the sky was partly cloudy, and the sun shone occasionally on the clusters. One 2007 cluster (A2) diminished somewhat through

time because the colony was gradually moving down the arroyo, which is typical with the advance of winter (Calvert & Brower 1986). In 2008 the weather was clear throughout the experiment, and the clusters did not change in size during the course of the experiment.

Analyses. We performed statistical analyses with SPSS 14.0 (SPSS Inc.) separately for each year. Comparisons of the measurements inside and outside each cluster were made by one-tailed paired t-tests, with arcsin transformation of relative humidity data, and the results were evaluated with a modified Bonferroni correction for multiple tests (Walsh 2004). Error bars used in the figures are 95% C.I. about the means (± 1.96 S.E.). Data from both years were analyzed identically except that calibration of the hygrochrons for the 2008 measurements ensured that pairwise comparisons of their readings were more accurate.

RESULTS

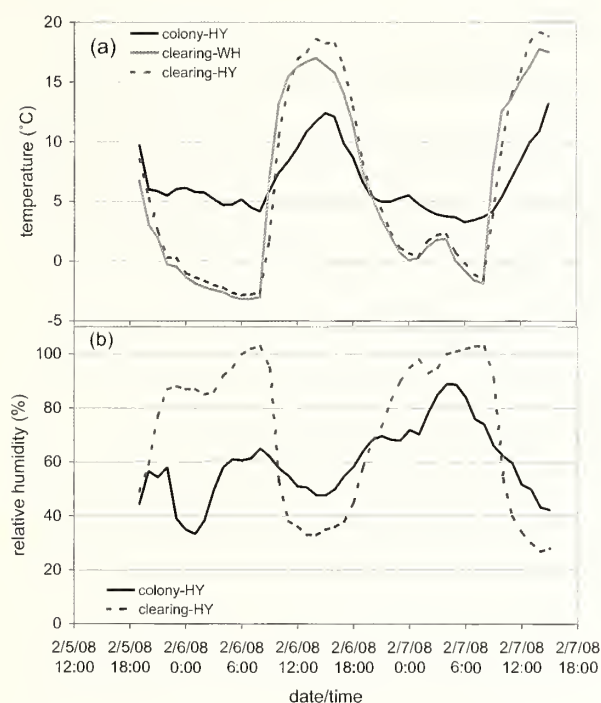


FIG. 6. Records of (a) temperature and (b) relative humidity from within the colony (average of three ambient hygrochrons) and from a clearing at the MBBR Field Station on the Llano de las Papas, Sierra Chincua, Michoacan, Mexico. The records from the clearing are given as recorded by both the Weather-Hawk weather station (WH; temperature only) and by a hygrochron attached to the weather station (HY). Data were recorded 5–7 Feb 2008 during three clear days. The variation in temperature and RH is much less within the colony than in the clearing, and the inverse relationship between temperature and RH is apparent. Humidity in the clearing ranges from 100% during the night to a drying 27% during the day.

Weather. During the 2008 experiment, records from the nearby Chincua weather station (Fig. 6) revealed a much greater range in temperature and RH (from -3.2° to 17.8°C and 27% to 100%) than was recorded in and around the monarch clusters ($+3.3^{\circ}$ to 13.2°C and 33% to 89%), which were in dense forest and thus less exposed. With the absence of precipitation during the very clear three days of recording, data measured at the weather station showed temperature and relative humidity to be inversely proportional (Fig. 6 a, b), as expected. Wind speed within the colony during our study gave five-minute averages up to 2.7 m/s, with gusts up to 3.8 m/s. Wind was highest during the afternoon, but even at night, wind was consistently more than 1.0 m/s.

2007 Experiment. Following the initial experiment in 2007, measurements of temperature and relative humidity were analyzed without calibration, and the results suggested microclimatic buffering within the clusters. The inside of cluster A1 remained significantly warmer at night ($t=6.491$, $df=49$, $p<0.001$), although this night-time difference did not hold for cluster A2. The differences in RH at night were mixed. Microclimatic buffering was conspicuously greater, however, in the daytime. Both clusters remained significantly cooler inside than outside by up to 0.3°C (Fig. 7; cluster A1: $t=7.682$, $df=22$, $p<0.001$; cluster A2: $t=3.879$, $df=20$, $p=0.001$). Coinciding with lower temperatures, both clusters also maintained significantly higher humidity inside (Fig. 8; cluster A1: $t=1.903$, $df=22$, $p=0.035$; cluster A2: $t=3.270$, $df=20$, $p=0.004$). The separate ambient sensor (A3) recorded up to 0.7°C colder temperatures at night and morning than did the

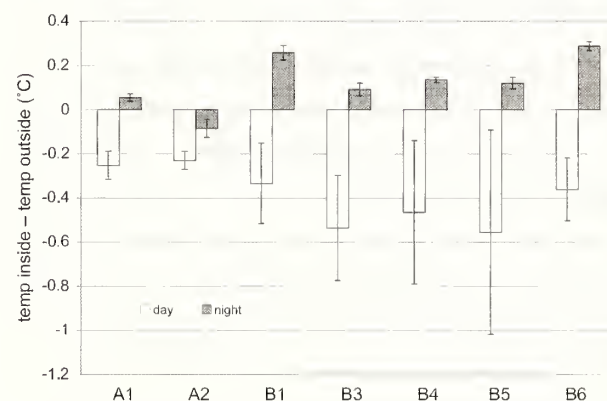


FIG. 7. Differences in temperature across the clusters. The inside minus the outside temperature is shown, averaged over all readings for each separate cluster, with error bars indicating the 95% C.I. for the means. The two 2007 clusters (initial experiment) are labeled A, and the five 2008 clusters are labeled B. In all cases, the inside of the clusters remained significantly cooler than the outside during the day (open bars), while 6 of the 7 clusters were significantly warmer at night (shaded bars).

sensors on the outside of the clusters, whereas it recorded up to 0.3°C warmer temperatures during the afternoon and evening. Even though thermal buffering was greater inside the clusters, the outside of the clusters experienced slightly more moderate conditions than ambient temperatures closer to the forest floor.

2008 Experiment. Before analyzing the 2008 data, we calibrated the hygrochrons separately for warm and cold temperatures, with readings of one hygrochron adjusted to match the measurements from the lab tests of the other hygrochron. The precision of the temperature readings was higher than that of the relative humidity readings. Temperature adjustments for the five hygrochron pairs ranged from 0.06° to 0.11°C for warm (day) data and from 0.11° to 0.16°C for cold (night) data. Adjustments for relative humidity ranged from 0.35% to 0.55% in warmth and from 0.93% to 1.07% in cold.

Using these calibrated measurements, the five clusters gave consistent results over the two days of

measurement (Figs. 7, 8). During the cold night hours, the inside of the clusters was significantly warmer than the outside for all five clusters (and six of the seven night measurements, with the seventh showing the same trend, Table 1). The difference between the inside and the outside declined during the long night hrs (Fig. 9). Three clusters (over four separate night comparisons; Table 1) had significantly higher RH inside despite the warmer temperatures, which would usually lead to lower RH. One cluster (B1) recorded lower RH, while there was no difference in another (B4).

As with the 2007 results, microclimatic effects were stronger during the warm afternoon hours. During daytime, the inside of the clusters remained significantly cooler than the outside for all five clusters (and eight of the ten separate comparisons, with the other two showing the same trend, Fig. 8, Table 1). Also, the inside of the clusters maintained significantly higher RH than the outside for all five clusters (and nine of the ten separate comparisons, a response reciprocal to that of

TABLE 1. Statistical results of all 2008 measurements, showing comparisons of the outside and inside readings of temperature and relative humidity from each monarch cluster. The comparisons for each of the five clusters (B1, B3, B4, B5, B6) have been separated for each day and each night in this table. Two days and two nights were analyzed for each cluster, except for clusters B4–B6, for which data were available for a single night. Analysis by paired t-tests was evaluated with modified Bonferroni correction for each set of comparisons.

Comparison			Temperature				Relative Humidity				
cluster	date	location of highest readings	t _c	d.f.	P	sig.	location of highest readings	t _x	d.f.	P	sig.
day/warm											
B1	6Feb08	outside	3.066	15	.008	°	inside	2.777	15	.014	°
B1	7Feb08	outside	3.054	8	.016	°	inside	4.588	8	.002	°
B3	6Feb08	outside	5.139	15	.000	°	inside	4.577	15	.000	°
B3	7Feb08	outside	9.702	8	.000	°	inside	4.135	8	.003	°
B4	6Feb08	outside	4.012	15	.001	°	inside	3.795	15	.002	°
B4	7Feb08	outside	2.075	8	.072	n.s.	inside	3.243	8	.012	°
B5	6Feb08	outside	3.423	15	.004	°	inside	1.808	15	.091	n.s.
B5	7Feb08	outside	2.135	8	.065	n.s.	inside	3.128	8	.014	°
B6	6Feb08	outside	4.768	15	.000	°	inside	4.802	15	.000	°
B6	7Feb08	outside	6.097	8	.000	°	inside	4.302	8	.003	°
night/cold											
B1	6Feb08	inside	16.749	27	.000	°	outside	5.547	27	.000	°
B1	7Feb08	inside	7.346	27	.000	°	outside	2.697	27	.012	°
B3	6Feb08	inside	2.511	27	.018	°	inside	3.888	27	.001	°
B3	7Feb08	inside	1.452	27	.158	n.s.	inside	3.013	27	.006	°
B4	7Feb08	inside	23.991	27	.000	°	same	0.352	27	.727	n.s.
B5	7Feb08	inside	7.544	27	.000	°	inside	5.651	27	.000	°
B6	7Feb08	inside	26.071	27	.000	°	inside	13.551	27	.000	°

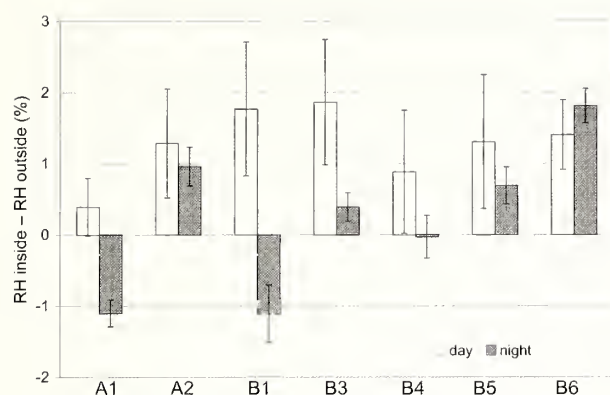


FIG. 8. Differences in relative humidity across the clusters. The inside minus the outside RH is shown, averaged over all readings for each separate cluster, with error bars indicating the 95% CI for the means. The two 2007 clusters (initial experiment) are labeled A, and the five 2008 clusters are labeled B. In all cases, the inside of the clusters remained more humid than the outside during the day (open bars), while 4 of the 7 clusters were significantly more humid at night (shaded bars).

temperature (Fig. 9, Table 1). The sensors in the control bough (B7) averaged 0.13°C warmer during the 12 hrs of day and 0.11°C warmer during the 12 hrs of night than the outside of the boughs with monarchs. These small differences suggest that the conditions immediately outside of the clusters were accurate representations of the ambient conditions at the same height within the forest.

DISCUSSION

The results found in 2008 support those suggested by the 2007 data: monarchs on the inside of clusters experienced warmer temperatures at night, cooler temperatures during the day, and elevated relative humidity throughout both day and night.

The coldest temperatures occur during night and early morning hours, so these are the times when microclimatic buffering against freezing comes into play. Significant buffering against cooler temperatures occurred throughout the 0000–0800 hr night period. Insulation against freezing would be most important for the butterflies in the clusters during the coldest moments, which occur when cloud cover opens up after winter storms and when cold air flows through the colony. While a difference of 0.1° to 0.2°C will not substantially affect the probability of monarchs freezing when they are dry, a combination of wetness and freezing temperatures during and immediately after winter storms strongly lowers their survivorship (Anderson & Brower 1996; Brower *et al.* 2004). Denser clusters, which frequently occur in years with larger

colonies, would likely increase the insulative effect.

Thermal buffering was stronger during daylight hours, with experimental clusters remaining cooler on the inside during peak warmth. Some variation exists among clusters because of different exposure to sunlight. The temperature differences are small, ranging up to 0.6°C ; however, by lowering the warmest temperatures, these differentials may reduce metabolic rate by approximately 6.4% and the consequent consumption of critically limited lipid reserves (Masters *et al.* 1988). We estimated the lipid savings by assuming: (1) the empirical relationship between body temperature and metabolic rate as measured for adult California monarchs (Chaplin & Wells 1982); (2) an average weight for an overwintering butterfly of 530 mg (Calvert & Lawton 1993); (3) a temperature reduction of 3.6 degree-hrs per day (equivalent to 0.6°C for 6hr); (4) a 150 day overwintering period; and (5) the calm early February conditions under which this study was conducted. With these assumptions, the lipid savings for the overwintering season were small, ranging from 2 mg in a cold winter to 4 mg in a warm winter. These savings are in context of the average lipids in November being 129 mg per butterfly (unpubl. data). However, as ambient temperatures rise in late February and March, the thermal insulation of the inside of clusters may increase and thus produce greater lipid savings. Also, even small savings could affect those monarchs that arrive low in lipids by providing them with critical energy that they need to fly to water and to remigrate at the end of the overwintering season. A savings of a few mg of lipids could have a significant effect on survival.

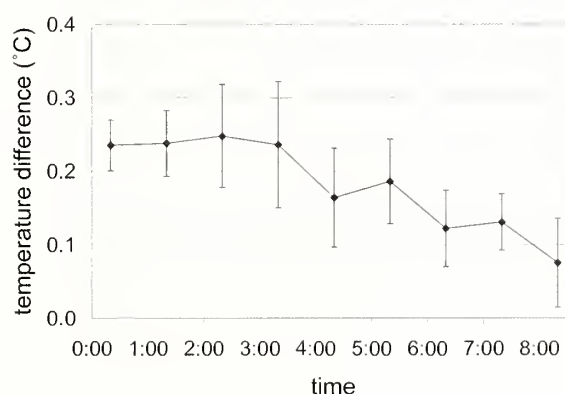


FIG. 9. Temperature difference between the inside and outside of the clusters through the night (0000–0840 hrs). The inside minus the outside temperature is shown, with error bars indicating the 95% CI for the mean each hour; the data show the average difference for three measurements each hour (e.g., 0000, 0020, and 0040 combined for 0020 hr) across all five 2008 clusters, with measurements recorded during 2 nights for clusters B1 and B3 and for 1 night for clusters B4–B6 ($n=21$ for each data point). The difference decreased by morning.

Relative humidity was higher by up to 3% inside all clusters during the day and higher at night in most, despite the temperature also being higher on the inside. Increased humidity reduces the threat of desiccation, an ever-present hazard when available moisture is limited, as is the case in the overwintering habitat as the dry season progresses. Part of the elevated humidity could have been due to evaporative transpiration from the fir needles within the butterfly clusters.

A greater range of temperature and relative humidity was found outside the clusters than inside. It is striking that structures as thin and seemingly delicate as butterfly wings provide insulation against environmental fluctuations, but when many wings are grouped together densely, as in the overwintering monarch colonies, the reason becomes clear. Still air is such a highly efficient thermal insulator that most heat exchange occurs through convective air movement, rather than through conduction. The microclimatic buffering in butterfly clusters derives from their wings trapping pockets of air that remain still, an effect that may have been supplemented by the fir bough needles. Single layers of butterflies serve as baffles that slow cross-wise air movement, while dense, multilayer clusters produce a quilt-like layer of insulation that blocks the convective exchange of heat between the outside and inside of a cluster. This effect would likely be even stronger during unstable weather when their wings also block winds.

Our results are based on comparisons of temperature and relative humidity inside and immediately outside the monarch clusters, and, as such, they do not distinguish potential microclimatic buffering provided by the fir needles from that created by the butterflies. It is likely, however, that the effect of the bough *per se* is less than the effect of the butterflies because most heat exchange is by convection, and air movement would be restricted more by a dense mass of butterfly wings than it would by an open bough of needles. The bulk of the microclimate differences inside and outside the clusters was likely from insulation produced by the densely packed butterflies, perhaps supplemented by buffering by the fir needles.

It is likely that the microclimatic advantages of clustering are diminished by even moderate forest thinning that results in colder nights (Calvert *et al.* 1984) and very likely warmer days. Unfortunately, illegal forest thinning, clear cutting, and burning of the clear cuts have become increasingly widespread in the Monarch Butterfly Biosphere Reserve (Brower *et al.* 2002; Ramirez *et al.* 2003, 2006; Honey-Roses & Galindo 2004; WWF-Mexico 2006; Brower *et al.* 2008).

It is also likely that larger clusters provide greater

microclimate protection of the butterflies than smaller ones. During the 1990's, one of us (LPB) witnessed enormously dense clusters in the Cerro Pelon colony, but has not seen such densities for several years. If the numbers of monarchs overwintering in Mexico continue to decrease, as is suggested by data from the last 15 yr (Rendon-Salinas *et al.* 2008), the average densities and cluster sizes may diminish along with a substantial measure of the microclimatic advantages of clustering that we have demonstrated.

CONCLUSIONS

Our results support the hypotheses that the clustering behavior of monarch butterflies on tree branches in their overwintering aggregations provides them with three microclimatic advantages, possibly enhanced by the fir boughs themselves: (1) buffering against lower temperatures during cold nights, thus lowering the probability of the butterflies inside the clusters freezing; (2) buffering against heating during warm days, thus reducing the rate at which the internal monarchs consume their lipid stores; and (3) maintaining higher humidity inside the clusters, thus lowering the rate of desiccation of the butterflies. While small, each of these factors contributes to a constellation of microclimatic advantages of clustering.

This study took place under moderate weather conditions. When clearing follows wet winter storms, however, the temperature inside the forest can plunge to as low as -5°C (Calvert *et al.* 1983), which leads to extensive mortality (Brower *et al.* 2004). Had this experiment been done under these conditions, it is likely that the magnitude of the temperature differences inside and outside the clusters would have been greater. Likewise, the advantage of clustering in maintaining higher humidity will most certainly be greater as the dry season advances and the weather becomes increasingly warm and dry.

The architecture of the short needled oyamel fir branches allows the butterflies to consolidate into larger and more dense bag-like clusters than possible on the flat needled cedars or the long needled pines (Figs. 2, 3). Because of the microclimatic advantages of clustering on boughs, there may be competition among individuals to position themselves toward the center of the clusters. More detailed studies of cluster architecture, butterfly clustering behavior, and possible microclimate advantages enhanced by the tree species upon which the butterflies form their clusters are needed.

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COMPARATIVE SUCCESS OF MONARCH BUTTERFLY MIGRATION TO OVERWINTERING SITES IN MEXICO FROM INLAND AND COASTAL SITES IN VIRGINIA

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ABSTRACT. Prior tagging studies at Atlantic coastal sites in New Jersey and Virginia suggested that fall migrant monarch butterflies (*Danaus plexippus* L., Nymphalidae: Danainae) of the eastern North American population have lower recovery rates at overwintering sites in Mexico compared to the overall recovery rates reported by Monarch Watch for monarchs tagged throughout the late summer breeding range. Here we present the results of the first quantitative study that compares the probability of recapture in Mexico of monarchs tagged at coastal sites with inland sites that are east of the Appalachian Mountains. During the 2001–2006 fall migrations, we tagged 1,008 monarchs along the Appalachian piedmont in Virginia, of which 13 (1.29%) were recovered in Mexico. In contrast, out of 1,216 tagged at Atlantic coastal locations in Virginia, only 2 (0.16%) were recovered. This eightfold lower recapture rate of the coastal monarchs is highly significant. The data also indicated that monarchs migrating along the piedmont on the eastern side of the Appalachians are nearly as likely to reach Mexico as are those that migrate west of the Appalachians. We conclude that migrating along the Atlantic coast per se is more risky than migrating inland either east or west of the Appalachians. The recovery data also determined that both sexes of the piedmont migrants reached Mexico, but, for unknown reasons, females were more successful. Since coastal migration occurs regularly and involves very large numbers of monarchs, the Atlantic coast is not an aberrant migratory route as the Urquhart maintained. Why then do fewer coastal migrants reach Mexico? Some continue southward and may become incorporated in and help sustain breeding populations in south Florida, Cuba and perhaps in other Caribbean islands and the Yucatan. To explore other possible reasons for the lower success of coastal monarchs in reaching Mexico, we compared wing lengths and wet masses of 483 inland with more than 140 coastal monarchs. The latter had slightly but significantly smaller wing lengths and, even after accounting for variation in wing length, they weighed less than the inland monarchs. The lower wet mass reflects lower lipid and/or lower water contents which we argue may be a consequence of anthropogenic degradation of much of the native flora and nectar sources along the Atlantic coast. We consider various hypotheses that may account for the coastal migrants' smaller wings than the inland migrants, including the controversial idea that the longer winged migrants may be blown out to sea.

Additional key words: tagging and recapture rates, wet mass, wing length, nectar availability; Atlantic coastal ecosystem deterioration, risky fall migration route.

Qualitative knowledge derived from the recoveries of tagged fall migrant monarch butterflies (*Danaus plexippus*, L.) has indicated that their success in reaching the overwintering areas in Mexico is substantially greater when the butterflies are tagged west compared to those tagged east of the Appalachian Mountains (Urquhart & Urquhart 1979a, b; Urquhart 1987; Monarch Watch 2006). An unexplored aspect of this difference is whether monarchs migrating along the Atlantic coast per se have a lower probability of reaching Mexico, or whether all monarchs migrating east of the Appalachians, including the piedmont and the coastal areas, are less successful.

To obtain quantitative data on the fall migration along

the Atlantic coast, Walton (1999), Walton & Brower (1999) and collaborators initiated a tagging program in Cape May Point, New Jersey. In the fall of 1998, they tagged 7,541 monarchs (number corrected by Brower *et al.* in prep), of which seven were subsequently found at the Mexico overwintering sites, a recapture frequency of 0.093%. In 1998 Garland & Davis (2002) started a second coastal tagging program on the southern tip of the Delmarva Peninsula in Virginia. They released 2,190 monarchs over three years (1998–2000), of which one was found in Mexico, a recapture frequency of 0.046%. In contrast, of an estimated 1.1 million monarchs tagged by Monarch Watch participants from 1992 through 2006 in the eastern US and southern

Canada, 12,000 to 14,000 were recaptured in Mexico, a recovery rate of 1.09% to 1.27% (Taylor pers. com. 2007; Monarch Watch 2006). Using Monarch Watch's lowest recovery rate as a rough estimate of the overall eastern rate and dividing it by each of the above coastal rates ($1.09\% / 0.093\% = 11.7$; and $1.09\% / 0.046\% = 23.7$) indicates that the coastal monarchs have only 1/12th to 1/24th of the chance of being recaptured in Mexico (see also Taylor, in McNeil 2006).

This much lower probability of coastal monarchs reaching Mexico raises four questions that we address in this paper. First, are all monarchs that migrate along the eastern side of the Appalachians less likely to reach Mexico than monarchs that migrate west of the Appalachians? Or, second, do those monarchs that migrate along the piedmont that stretches eastwards from the Appalachians to the coastal plain (Atwood 1940; Raisz 1957) have a success rate similar to migrants west of the Appalachians? Third, if the coastal migrants per se are less successful, do these monarchs exhibit differences in physical properties from the inland piedmont migrants? Fourth, if there are physical differences between the coastal and inland piedmont

monarchs, what factors might account for the differences?

To answer the first two questions, we compared the number of recaptures in Mexico of monarchs collected and tagged along the eastern edge of the Appalachian piedmont in northern Virginia with recaptures of monarchs collected and tagged during the same years along the Atlantic coast in southern Virginia. We addressed the third question by comparing wing lengths and adult weights (wet mass) of sub-samples of the tagged inland and coastal monarchs. We addressed the fourth question by relating the wing length findings to greater coastal losses due to wind and possible other causes, and by relating the wet mass findings to anthropogenic changes in habitat quality along the Atlantic coast.

MATERIALS AND METHODS

Collecting sites. Over six years (2001–2006) between the last week of August and the last week of October, Brindza collected fall migrant monarchs from one or more coastal and inland sites in Virginia. The collection dates overlapped with the timing of the fall

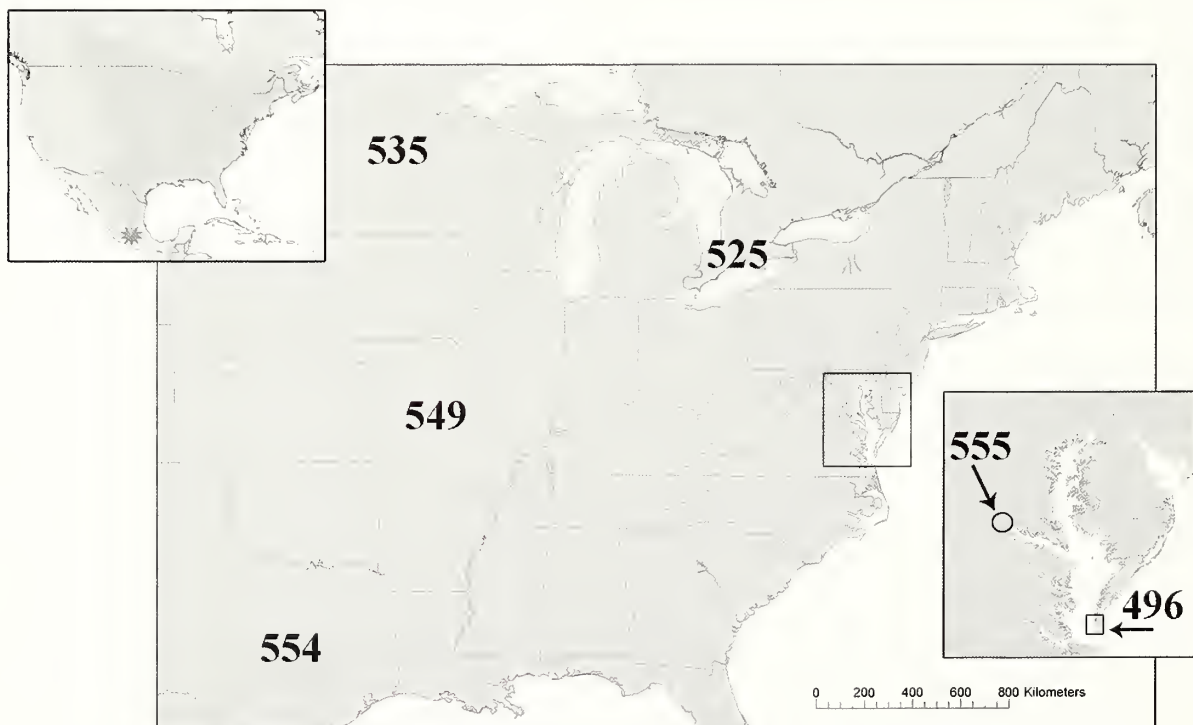


FIG. 1. Location of coastal and inland study sites in eastern Virginia and average wet masses of fall migrant monarchs in eastern North America. The coastal sites were located on the southern tip of the Delmarva Peninsula (small square in the lower inset box). The inland sites were centered around the town of Woodbridge on the piedmont of the Appalachians (small circle in the lower inset box). The numbers on the map indicate average wet masses (mg) of males and females combined of fall migrant monarchs from this study and from other published studies (Brown and Chippendale 1974; Gibo and McCurdy 1993; Borland *et al.* 2004). The upper left inset shows the approximate range of the eastern North American monarch population, with the location of the Mexican overwintering area.

migration along both the Atlantic coast in Virginia (Garland & Davis 2002; Gibbs *et al.* 2006) and through an inland site on the eastern edge of the Blue Ridge Mountains at Sweet Briar College, Virginia, about 275 km west of the coastal area (Brower *et al.* 2006). In the fall of 2001, Brindza concentrated on tagging the butterflies and, from 2002 through 2006, he also weighed and measured the forewing lengths of sub-samples of those that he tagged and released.

The coastal samples were collected at Kiptopeke State Park, on the Eastern Shore of Virginia National Wildlife Refuge and Fisherman Island National Wildlife Refuge. These areas are surrounded to the west by Chesapeake Bay and to the east and south by the Atlantic Ocean (Fig. 1). Both are good locations for capturing migrating monarchs because of the funneling effect of the peninsula (Garland & Davis 2002).

The inland monarchs were collected along the Piedmont about 190 km northwest of the coastal area within a 10 km radius of Woodbridge, VA (38° 38' 08" N, 77° 15' 44" W), 20–30 km SW of Washington, D.C. (Fig. 1.). The collecting site in 2001 was solely in Lorton, while from 2002–2006, the butterflies were collected in Lorton, Gunston Cove, the Occoquan Bay National Wildlife Refuge and Mason Neck State Park.

Collecting methods. Brindza netted most monarchs while they were nectaring on several species of composites growing in open fields or in flowerbeds, and on cultivated and native shrubs. About 2% were collected from roosts. Immediately after capture, he removed each monarch from the net and placed it in a 5.1 × 7.6 cm glassine envelope. Successive captures were accumulated for about 10 minutes in a small plastic box and kept out of direct sunlight.

Brindza made all plant identifications based on Newcomb (1977), Peterson & McKenny (1968) and Lobstein (1990). We followed the USDA plant data

base to standardize the common and scientific nomenclature (Anon. 2007a). Composites (Asteraceae), on which many butterflies were nectaring, included bearded beggar ticks (*Bidens aristosa* (Michx.) Britt.), woodland sunflower (*Helianthus divaricatus* L.), bull thistle (*Cirsium vulgare* (Savi) Ten.), other thistles (*Cirsium* spp.), false boneset (*Brickellia eupatorioides* [L.] Shinnery), white snakeroot (*Eupatorium rugosum* = *Ageratina altissima* (L.) King & H.E. Robins), seaside goldenrod (*Solidago sempervirens* L.), *Solidago* spp., hyssopleaf thoroughwort (*Eupatorium hyssopifolium* L.), late flowering thoroughwort (*Eupatorium serotinum* Michx.), orange cosmos (*Cosmos sulphureus* Cav.) and garden cosmos (*C. bipinnatus* Cav.). The shrubs on which they were nectaring included butterfly bush (*Buddleia davidii* L., Buddleiaceae), Russian olive (*Elaeagnus angustifolia* L., Elaeagnaceae), abelia (*Abelia abelia* R. Br., Caprifoliaceae), lantana, (*Lantana camara* L., Verbenaceae) and groundsel tree (eastern baccharis, *Baccharis halimifolia* L., Asteraceae).

Tagging. Brindza tagged the butterflies within 10 minutes of capture using numbered adhesive tags provided by Monarch Watch. Over the six years, he tagged and released 1,216 monarchs in the coastal sites and 1,008 in the inland sites (Table 1). We subsequently determined those recovered at the overwintering sites in Mexico by consulting the Monarch Watch tag recovery data base (<http://www.monarchwatch.com/tagmig/recoveries.htm>).

Weighing and measuring. During 2002–2006, Brindza measured the left forewing length and wet mass of sub-samples of the monarchs that he tagged (Figure 2). He measured left forewing length following the protocol of Brower & Van Hook (in prep.). This measure (mm) the straight line distance on the ventral surface of the forewing from the forewing tip to the white dot on the base of the wing where the wing

TABLE 1. Summary of the number of monarch butterflies tagged during this study at coastal and inland sites in Virginia.

Year	Coastal				Inland				Grand Total
	Males	Females	Total	% Female	Males	Females	Total	% Female	
2001	231	182	413	44.1	374	151	525	28.8	938
2002	67	18	85	21.2	41	22	63	34.9	148
2003	34	20	54	37.0	35	21	56	37.5	110
2004	7	4	11	36.4	2	0	2	0.0	13
2005	14	17	31	54.8	99	64	163	39.3	194
2006	370	252	622	40.5	134	65	199	32.7	821
Total Tagged	723	493	1216	40.5	685	323	1008	32.0	2224

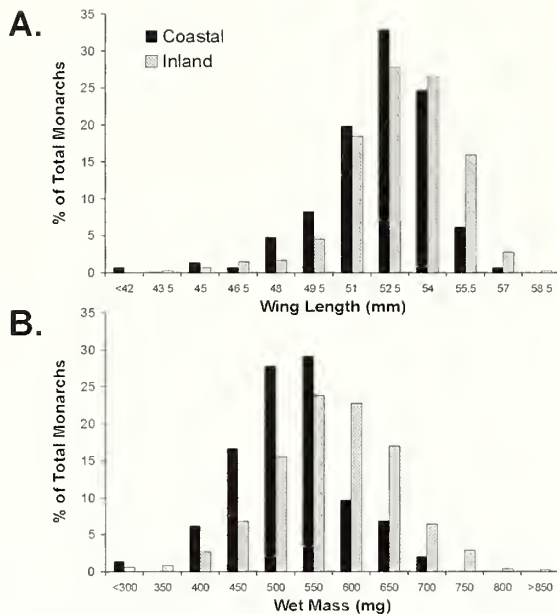


FIG. 2. Distribution of (A) forewing lengths (mm) and (B) wet masses (mg) of the coastal and inland monarchs.

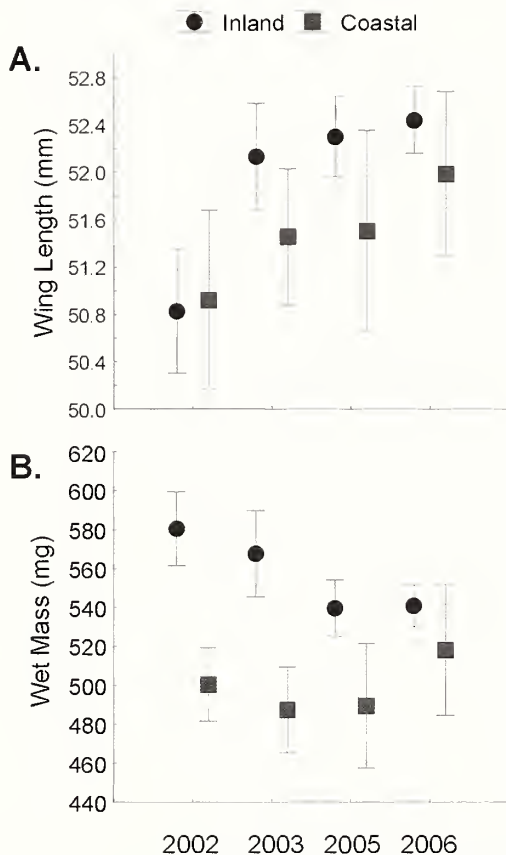


FIG. 3. (A) Average wing length and (B) average wet mass of monarchs for the four years (2002–2006, excluding 2004) for both inland and coastal sites. Bars indicate 95% confidence intervals.

attaches to the thorax. All measurements were made to the nearest 0.1 mm with handheld Mitutoyo digital calipers (Ben Meadows Co., Janesville, WI). Brindza also measured wet mass, rounded to the nearest mg, using a portable electronic balance with an accuracy of 0.001 g (Acculab, Model PP2060D, Sartorius Group, Göttingen, Germany). The balance was recalibrated on each day of use. Throughout the study, the length of time between capture and measuring and weighing individual monarchs did not exceed 15 minutes. Weighing them as soon as possible after capture is imperative to avoid mass (weight) loss through desiccation.

Statistical analyses. We used Statistica 6.1 software (Statistica 2003) for our analyses. We used chi-square to test for significant differences in the numbers of recaptures in Mexico of monarchs tagged at the inland vs the coastal sites. We also used chi-square to test for differences in the numbers of tagged males and females in reaching Mexico. We used ANOVA to explore the factors influencing variation in monarch wing lengths and wet masses. With wing length or wet mass as the dependent variable, we included site (inland and coastal), sex (male and female), and year (2002, 2003, 2005 and 2006) as categorical independent variables. The 2004 data were excluded from the analyses because of the very small sample sizes. All two-way and three-way interactions were initially included in the model, and dropped if not significant. We used analysis of covariance to examine the factors affecting monarch mass, with wing length as a covariate to account for the fact that mass is influenced by butterfly size (*i.e.* forewing length).

RESULTS

Recaptures in Mexico. Thirteen of the 1,008 (1.29%) butterflies tagged at the inland sites were recaptured while only 2 of 1,216 (0.16%) were recaptured from the coastal sites (Tables 1 and 3). This eight-fold difference in recapture rate is statistically significant (chi-square = 10.41, 1 df, $P < 0.001$). Our data thus indicate that monarchs migrating inland across the piedmont east of the Appalachians have a much higher probability of being recaptured in Mexico than do those migrating along the Atlantic coast.

Our low coastal recapture rate was 1.8 times higher than that found by Walton & Brower (1999) in Cape May (0.093%) and 3.6 times higher than that found by Garland and Davis (2002), on the southern tip of the Delmarva Peninsula in Virginia (0.046%). Our higher value is likely due to the fact that the majority of our monarchs were tagged during the fall preceding the January 2002 storm that killed nearly one quarter of a

billion monarchs in two colonies (Brower *et al.* 2004) and resulted in an all time high tag recovery rate in Mexico (Monarch Watch 2006).

There was a deficiency of females each year in all samples except for the coastal sample in 2005 (Table 1). For the inland samples tagged in 2001, there were 374 males and 151 females, *i.e.* 29% females. Of the 12 inland monarchs recaptured in Mexico that season, 7 of 12, *i.e.* 58% were females. Thus there was a reversal in the sex ratio with twice the frequency of tagged females recaptured (chi-square = 5.12, 1 d.f., $P < 0.025$) indicating that both sexes reached Mexico from the inland route, but that females were substantially more successful than males in doing so.

Wing length. The data for the coastal and inland samples are shown in Figs. 2A and 3A. Two way ANOVA (Figure 4) analyzed differences for site, year and sex for the 617 monarchs that we measured. We found no significant ($P > 0.10$) two-way interaction terms. When these were dropped, the main effects revealed significant effects of both year ($F_{3,611}=10.5$, $p<0.001$) and site ($F_{1,611}=4.0$, $p=0.046$). Tukey's post-hoc comparisons indicated that monarchs captured in 2002 were significantly smaller than in all other years. The effect of site is evident in Figure 3A, with monarchs slightly but significantly larger at the inland sites on average and for three of the four years. At the inland sites, the average for both sexes was 52.1 mm, while at coastal sites it was 51.3 mm, a difference of about 1.5%.

Body mass. The data for the coastal and inland samples are shown in Figs. 2B and 3B. For wet body mass, the final model contained several highly

significant main effects and interaction terms (Table 5), most notably, the main effects of year ($F_{3,602}=8.6$, $p<0.001$), sex ($F_{1,602}=4.4$, $p<0.037$), and wing length ($F_{1,602}=182.5$, $p<0.001$). Males weighed significantly more than females (Table 2B), 552 mg vs 511 mg overall), and not surprisingly, the effect of wing length was positive (*i.e.* monarchs with longer wings also had greater mass). There was a significant interaction of site*year ($F_{3,602}=5.7$, $p=0.001$, Table 5). This interaction effect is evident in Fig. 3B, in that the monarchs from the coastal site weighed less than those from the inland, but the magnitude of this effect depended on the year, being smaller in 2006 than in 2002. Further, the difference in wet mass between sites was not due to the size difference in monarchs, as indicated by an analysis of covariance in which the effect of wing size was included in the mass model. To elucidate this point further, we plotted (Fig. 4) the average residual mass (from the significant linear regression of mass *versus* wing length) of both sites so that the difference in weights, after wing length is accounted for, can be seen. Thus when size is removed, the difference in mean residual mass between sites is significant (t-test, $df = 625$, $t = 2.31$, $p = 0.021$). Thus the average wet mass of the coastal migrants (496 mg) was 9.6% less than the inland migrants (549 mg) and was lower than that found in several other studies (Brown & Chippendale 1974; Gibo & McCurdy 1993; Borland *et al.* 2004) as shown in Figure 1.

DISCUSSION

The data from this study in Virginia demonstrate that monarchs captured during the fall migration along the Atlantic coast differed in three significant ways from those migrating inland across the piedmont between the Appalachians and the coast. Relatively few of the coastal migrants succeeded in reaching the overwintering sites in Mexico, they had slightly smaller wing lengths and they had lower wet masses. These results have major implications for a more complete understanding of the fall migration of the eastern North American population of the monarch butterfly.

Migration east and west of the Appalachians. Based on their tagging studies, Urquhart & Urquhart (1979a, b) and Urquhart (1987) maintained that monarch migration along the Atlantic coast is "aberrant". Briefly, they contended that variable numbers of fall migrants are blown by westerly winds over the Appalachians to the east coast. They reasoned that these avoid flying over the ocean with most continuing to migrate south along the coast into Florida and thence into the Caribbean, without reaching the overwintering sites in Mexico. The Urquharts' aberrant

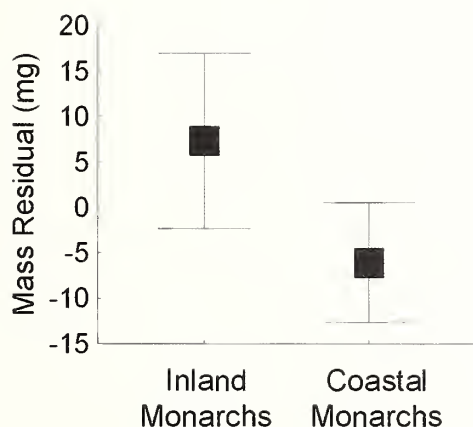


FIG. 4. Comparison of average residual mass (residuals from a linear regression of mass versus wing length) of monarchs from both inland and coastal sites. The difference is significant (t-test, $df=625$, $t=2.31$, $p=0.021$). Bars indicate 95% confidence intervals.

migration hypothesis, together with the much lower frequencies of recaptures in Mexico of monarchs tagged east compared to those tagged west of the Appalachians by Monarch Watch (Taylor pers. comm., 2007; Monarch Watch 2006), has led to the general assumption that monarch migration anywhere east of the Appalachians is a less successful strategy in reaching Mexico. This contention was reinforced by an analysis of 40 years of recapture data (Rogg *et al.* 1999) showing that migrants west of the Appalachians likely do get blown eastwards, but they are in some way able to compensate for this wind drift and, as some birds and dragonflies do (Richardson 1990; Syrgley 2004), they reorient to a southwesterly course leading them to Mexico (see also Howard 2007).

Based on the results of our study, this general model requires modification. We have determined that migration east of the Appalachians along the piedmont may be as successful as the migration west of the Appalachians. In contrast, as maintained in the past and

as we have confirmed, migration along the coast *per se* is far less successful. However, being less successful does not necessarily mean that the coastal migration is aberrant, a descriptor that we consider misleading.

Rejection of the aberrant migration hypothesis.

In contesting the aberrant coastal migration hypothesis, Walton & Brower (1996, 1999) reported that at least some tagged coastal monarchs do succeed in making it to Mexico, as we have again shown in this paper. Walton & Brower also reemphasized that the coastal migration has occurred regularly since it was described in the 19th century and often involves spectacular numbers of butterflies (Brower 1995). This has been confirmed quantitatively by fifteen consecutive annual censuses in Cape May, New Jersey begun in 1991 (Walton & Brower 1996; Walton *et al.* 2005) and by nine annual coastal censuses in Chincoteague, Virginia, 117 km south of Cape May (Gibbs *et al.* 2006). Further evidence of the large magnitude of the coastal migration includes reports of nocturnal roosts of over 10,000

TABLE 2. **A.** Female and male mean mass (wet weight) and size (wing length) comparisons between Coastal and Inland collections sites in VA. 2002-2006. **B.** Overall mean mass and size comparisons: **1)** Coastal versus Inland, combining all years and sexes and **2)** male versus female combining all years and both Coastal and Inland sites. Data for 2004 are not included because of very small sample sizes.

A.		WET WEIGHT (mg)				WING LENGTH(mm)			
		Females		Males		Females		Males	
		Coastal	Inland	Coastal	Inland	Coastal	Inland	Coastal	Inland
Year									
2002	Mean	449	557	524	593	49.9	50.7	51.3	50.9
	STD	49.7	83.3	54.4	68.1	2.3	2.1	2.7	2.1
	N	14	22	31	41	14	22	34	41
2003	Mean	495	539	483	585	52.1	51.9	51.1	52.3
	STD	59.8	65	77	88.4	1.4	1.1	2.0	1.9
	N	15	21	27	35	15	21	27	35
2005	Mean	487	507	492	561	52	51.8	50.9	52.6
	STD	84.6	95.9	93	88.2	2.2	2.5	2.4	1.9
	N	17	64	14	99	17	64	14	99
2006	Mean	521	514	516	554	52.3	52.3	51.8	52.5
	STD	43.2	77	72.7	73.8	1.7	2.1	0.9	2.0
	N	6	65	9	134	6	65	9	134
B		WET WEIGHT (mg)				WING LENGTH(mm)			
		Coastal	Inland			Coastal	Inland		
1. All Yrs & Both Sites	Mean	496	549			51.3	52.1		
	STD	71.4	85			2.2	2.1		
	N	133	481			136	481		
		Females	Males			Females	Males		
2. All Yrs & Both Sexes	Mean	511	552			51.8	52.1		
	STD	82.8	82.8			2.2	2.1		
	N	224	390			224	393		

monarchs on Chincoteague (Gibbs pers. comm.) and on Cape May (Smith 2007).

Given the fact that the Atlantic coastal migration is an integral part of the monarch's fall migration, what is the fate of migrants of the eastern North American population that do not make it to Mexico? Cardenolide fingerprinting indicated that some migrate into south Florida where they become incorporated into local breeding populations on the eastern edge of the Everglades (Knight 1998). Cardenolide fingerprinting together with isotope marker analyses determined that still others continue across the Caribbean to Cuba where they also become incorporated into local breeding populations (Dockx *et al.* 2004). Those that may reach the Yucatan or any of the Antillean islands (Urquhart 1987) may help sustain these tropical populations. However, the ability of all these butterflies to remigrate northwards the following spring is nil because, in becoming reproductive under the high tropical temperatures, they lose their migratory capacity and will not be able to live for the five or more months until spring arrives along the Gulf Coast (Brower 1995; Zemaitis 2005). On the other hand, some of those coastal migrants that regain the southwesterly migratory track do make it to the Mexican overwintering sites and have the opportunity to remigrate back into the southern USA the following spring.

In light of all these recent findings, we reject the aberrant migration hypothesis and we cannot agree with Taylor's contention (in McNeil Jr. 2006) that monarchs migrating along the coast are "lost." However, the lower recapture rates, shorter wing lengths and lower wet masses of the coastal migrants do indicate that there are negative factors affecting these monarchs' ability to reach Mexico. What might these negative factors be?

Risk of being blown out to sea favors shorter wing lengths. When one considers the distances the monarchs may fly, coastal migrants must be severely challenged by winds. The Atlantic coastal habitat extends for 2,700 miles from Maine to Florida, includes the Florida Gulf Coast, and continues westward and southward to the border of Texas and Mexico (Beatley *et al.* 2002). We propose that monarchs migrating along the coast have shorter wing lengths than those migrating inland because the larger individuals are more likely to get blown out to sea and have more difficulty flying back in than do the smaller ones. We are not advocating the idea that the coastal migrants are a sub-population that has been selected for shorter wing lengths. In fact, the likelihood of shorter wings genetically evolving is unlikely because of the random mating that occurs among the millions of individuals of the eastern population that takes place in Mexico (Brower 1995).

However, it is relevant to point out that natural selection is a strong evolutionary force that has shaped the flight dynamics of both birds and insects along coastal environments, and, on oceanic islands, has led to flightlessness in many lineages. It is also well established that insects lose control of their direction and velocity when they fly up out of the slower moving air in the boundary layer near the ground and can be carried away by the wind (pp. 298, 324, in Dudley 2000; Alexander 2002). However, Robert Dudley (pers. comm.), contends that the opposite should be true, namely that the larger winged individuals should have a better chance of fighting their way back in from the ocean to the coast. Dudley & Syrgley (2008) also found that several neotropical migrant butterflies reduce their flight speed as their lipid reserves deplete. Thus, there may be an interplay between size and mass in the coastal monarchs, resulting in the larger individuals that have a depleted lipid mass having to slow down, and therefore lowering their ability to fight the wind.

While we have no direct evidence, our wing length hypothesis is consistent with observations made by Schmidt-Koenig (1993) along the Atlantic coastline that monarchs avoid flying over large bodies of water unless the direction and speed of the winds are favorable. Gibbs (2007) also observed monarchs' strong reluctance to fly southwesterly across the Chesapeake Bay when the winds were unfavorable. That migrating monarchs are sensitive to unfavorable winds is also evident from their response to cross-winds by flying low to the ground (Schmidt-Koenig 1985; Davis & Garland 2002; Garland & Davis 2002), or by simply pausing their migration to wait for better conditions to resume flying and soaring (Schmidt-Koenig 1985; Davis & Garland 2004). Ishii *et al.* (1992), working along the Gulf Coast south of Tallahassee, Florida, counted the numbers of fall migrants that were flying over the ocean and found that the number flying inland exceeded the number flying out. They interpreted this as evidence for reluctance to sustain flight across the Gulf.

Energetically contending with the coastal environment. One hypothesis to explain the lower wet mass of the coastal monarchs compared with those collected inland is that excess exertion burns their lipids while they confront unfavorable beach winds and cross large bodies of water, including the numerous bays and sounds along the coast. Gibbs (in Gibbs *et al.* 2006; Gibbs 2007, pers. comm.) has studied coastal monarch migration through Chincoteague in Northern Virginia for 14 years (1994–2007) and she has frequently observed large numbers of monarchs being blown out to sea and others struggling against winds to return to land. She also noted that the butterflies that succeeded in

TABLE 3. Fifteen recoveries in Mexico of the 2,224 monarchs tagged by L. Brindza at inland and coastal sites in Virginia over five years (2001–2006). The tag cities are the towns closest to the tagging locations.

Sex	Tag Code	Tag City	Tag Date	Report Date	Wintering Colony
Inland					
Female	ABJ667	Lorton, VA	12-Sep-01	06-Jan-02	El Rosario
Male	ABJ835	Lorton, VA	22-Sep-01	26-Feb-02	El Rosario
Female	ABJ782	Lorton, VA	13-Sep-01	26-Feb-02	El Rosario
Male	ABJ388	Lorton, VA	04-Sep-01	26-Feb-02	El Rosario
Female	ABJ415	Lorton, VA	05-Sep-01	20-Feb-02	Sierra Chincua
Male	ABJ492	Lorton, VA	06-Sep-01	27-Feb-02	Sierra Chincua
Female	ABJ675	Lorton, VA	12-Sep-01	27-Feb-02	Sierra Chincua
Female	ABJ497	Lorton, VA	06-Sep-01	12-Mar-02	El Rosario
Female	ABJ484	Lorton, VA	06-Sep-01	24-Mar-03°	El Rosario
Female	ABJ682	Lorton, VA	12-Sep-01	03-Mar-04°	El Rosario
Male	ABJ538	Lorton, VA	07-Sep-01	18-Mar-05°	El Rosario
Male	ABJ757	Lorton, VA	13-Sep-01	18-Mar-05°	El Rosario
Male	HCM412	Woodbridge, VA	03-Sep-06	20-Feb-07	El Rosario
Coastal					
Female	AI1546	Cape Charles, VA	02-Oct-01	18-Mar-05°	El Rosario
Female	HCM160	Cape Charles, VA	03-Oct-01	06-Jan-07	El Rosario

°Time span greater than 1 overwintering season because tag was found and held by local residents until collected by Monarch Watch officials

returning immediately began nectaring. Louise Zemaitis (pers. comm.) has made similar observations in Cape May.

Beall (1948) found that many monarchs perished while attempting to cross Lake Erie during the fall and he determined that they had a lower lipid content than monarchs that survived the crossing. It therefore seems reasonable to conclude that migrants are forced to burn more lipid while using powered and flapping flight to contend with the coastal winds and flights across water than the tenfold more energy-efficient soaring and gliding that is common in the less windy inland environment (Schmidt-Koenig 1985; Masters *et al.* 1988; Davis & Garland 2004; Brower *et al.* 2006).

Are the diminished nectar resources and low lipid levels due to human encroachment? As implied by our having caught most of our butterflies at flowers, monarchs frequently interrupt their fall migration to drink nectar. Sugar that is contained in nectar is converted to lipid that the butterflies store and use to fuel their flight and other activities. In a recent study, Brower *et al.* (2006) found only moderate

amounts of lipids in migrating monarchs until they reach Texas, where they then accumulate large lipid stores. Lipid stores are critical to fuel the butterflies five month overwintering period in Mexico (Alonso *et al.* 1997).

We hypothesize that our coastal monarchs were lighter than the inland monarchs because they did not have access to sufficient nectar sources and that this is due to a diminished flora caused by habitat deterioration along the Atlantic coastal migratory corridor. While the overall nectar abundance may always have been less along the coast than inland, as now discussed, this is doubtful.

The coastal habitats. The dynamic ecological interrelationships of coastal habitats are described in Frid & Evans (1995). They include long ribbons of barrier and sea islands that over geological time developed a series of very different habitats extending from the sea to inland (Christensen 1988). The habitats include the sandy beaches, coastal prairies, primary and secondary sand dunes and wetland swales behind the dunes (Silberhorn 1999). Further inland are saline and

TABLE 4. Results of ANOVA model explaining variation in wing length of migrating monarch butterflies. The data for the 2004 year were not included in the analysis. All two-way interactions were initially included in the model but were removed when found not significant.

Independent	df	MS	F	P
Site	1	17	4.0	0.046
Year	3	46	10.5	<0.001
Sex	1	15	3.5	0.064
Error	611	4		
Total	616			

freshwater estuaries, lagoons, sounds and coastal forests. According to Delacourt & Delacourt (1981), this very dynamic ecosystem complex has persisted for the last 9000 years, about as long as the current monarch butterfly migration is thought to have existed (Brower 1995). Even though the various communities within this environmental can be complex and harsh (Barbour & Christensen 1993), they have specialized, productive and diverse floras (Barbour 1992; Tiner 1987, 1993; Packham & Willis 1997; Silberhorn 1999). These include numerous annual and perennial plants that serve as nectar sources for the monarch butterfly migrating through the complex of habitats each fall.

According to Bird (1985), coastal erosion through rising sea level has impacted about 70% of the planet's sandy beach environments including those along the North American Atlantic coast. Rising sea level causes the beach, coastal prairie and dune habitats to erode, but, with slow rising conditions, the habitats reestablish further inland. They then undergo ecological succession and the flora physically stabilizes the

TABLE 5. Results of ANOVA model explaining variation in wet mass of migrating monarch butterflies. The data for the 2004 year were not included in the analysis. The interactions of Site*Sex and Year*Sex were initially included in the model but were removed when found not significant.

Independent	df	MS	F	p
Site	1	8280	1.9	0.164
Year	3	36516	8.6	<0.001
Sex	1	18595	4.4	0.037
WingLength	1	778160	182.5	<0.001
Sex*WingLength	1	14502	3.4	0.066
Site*WingLength	1	12449	2.9	0.088
Site*Year	3	24216	5.7	0.001
Error	602	4263		
Total	613			

restored habitat. To what extent have humans diminished this environment?

Human encroachment. Human exploitation of the valuable economic resources offered by the dynamic coastal ecosystems and its severe impact on their natural features is documented in numerous studies (Turner *et al.* 1998; Doody 2002; Ray & McCormick-Ray 2003; Burroughs & Tebbins 2005; Feagin *et al.* 2005; Forman *et al.* 2005; Verhoeven *et al.* 2006; Martinez & Psuty 2007). The construction of buildings, dikes, parking lots, roads, etc. often squeezes the land against the ocean and blocks the natural inland sand movement. Sea currents then either wash the sandy beaches, the prairies and the dunes away, or reduce them to mere remnants with extensively diminished floras. It is estimated that 350,000 structures in the United States are located within 500 feet of the shorelines and nearly half of all coastal wetlands have been destroyed since pre-Columbian times (Beatley *et al.* 2002). Dredging and ditching in the first half of the 20th century also deteriorated much coastal habitat (Humphrey and Rockefeller 1968). Although passage of the 1972 Wetlands Act helped mitigate the losses, Beatley *et al.* (2002, p. 283) tell us: "Alarm bells are ringing everywhere as our coastal environment endures unabated development pressures and environmental degradation".

Another negative anthropogenic impact is the spraying of herbicides, including glyphosate ("Roundup", Monsanto, Inc., see Anon. 2005) and imazapyr ("Habitat", BASF Inc., see Anon. 2007b), to control marsh reed grass, *Phragmites australis* (Cav.) Trin. ex Steud. (Poaceae). These biocides, either directly or through inadvertent wind drift when applied by helicopters, can kill the nectar sources adjacent to the marshes. For example, spraying herbicides was a major issue in Cape May in 2005 (Fichter 2005) and in the Chincoteague National Wildlife Refuge in 2006. According to Denise Gibbs (pers. comm.), helicopter spraying on Chincoteague is forbidden if the wind exceeds 5 mph. However, on 2 October 2006—a peak monarch butterfly migration day—the spraying was continued with a 15 mph wind, drifting "Habitat" for at least a half a mile across a main *Solidago sempervirens* nectaring area. Yet other impacts are exemplified by helicopter spraying of malathion (see Anon. 2006) and by truck misting with the pyrethroid derivative resmethrin, ("Scourge", Aventis Environmental Science, see Anon. 2007c) for mosquito control by the Cape May County Mosquito Commission. A related synthetic pyrethroid ("Permethrin") has been found to kill monarchs in both larval and adult stages and has long term effects on the butterflies (Oberhauser *et al.* 2006).

The extent to which these various physical and chemical impacts have diminished the quantity and quality of the nectar sources in the coastal environment has not been quantified, but the losses have almost certainly affected the lipid and hydration dynamics of fall migrant monarch butterflies, as well as the nectar requirements of other animals living in and using this migratory corridor (Nabhan 2004; Brower & Pyle 2004).

Inland habitats. In contrast to the natural and anthropogenic hazards to monarchs flying along the coast, flight over the far more extensive inland routes with diverse and varied nectar resources may not be as stressful. Inland environments are also subject to less intense wind and, until recently, roadsides and agricultural fields provided extensive areas with wildflowers. Unfortunately, the ever-increasing use of herbicides on roadsides, and, in conjunction with the repeated spraying of corn and soybean crops that are genetically engineered to be resistant to the herbicides, are eliminating huge areas of floral resources (Brower *et al.* 2006).

Alternative hypotheses and future research. An alternative hypothesis to account for the smaller and lighter coastal monarchs is that fewer of their larvae had the opportunity to feed on *Asclepias syriaca* L. (Asclepiadaceae), the major food plant (Malcolm *et al.* 1989) of the monarch's eastern population and is known to be nutritionally superior to *Asclepias tuberosa* L. (Erickson 1973). The latter milkweed is widely distributed along the Atlantic coast (Woodson 1954), and it is possible that more of the coastal migrants had fed on it and ended up as smaller individuals. Thin layer chromatography analyses (Malcolm *et al.* 1989) could determine if the food plants eaten by the larvae differed among the larger and smaller individual butterflies. However, this explanation seems unlikely because, as implied above, the majority of coastal monarchs probably fed on *A. syriaca* plants growing inland before being wind-drifted to the coast.

Another possibility is that the smaller and lighter monarchs were less able than the larger and heavier ones to resist winds that blew them towards the coast. This is consistent with Beall's (1948) finding that the monarchs that drowned crossing Lake Erie were both smaller and lighter than ones he collected in roosts both north and south of the lake collections. Another possibility is that the monarchs with lower mass were more fuel and/or water stressed and therefore accumulated on the coast to nectar, while the heavier ones kept migrating south. It is important to remember that our samples were gathered in a very limited latitudinal transect. Much light could be shed on the questions by analyzing collections along the coast as the

migration progresses from Maine to Florida.

To test our habitat deterioration hypothesis, comparative measurements of the amount of nectar imbibed by monarchs (methods in Brower *et al.* in prep.) collected at inland and the coastal sites could be made. Currently, there are hundreds of citizen-scientists (Monarch Watch 2006; Prysby & Oberhauser 2004) who study, capture, tag and release monarchs each year. Direct measurements of wing length and wet mass, as done in this study without killing the individual monarchs, would help build long term comparative data sets. However, more accurate measurements of both lipid and water contents of the inland and coastal monarchs are needed. Wet mass is the sum of the water, lipid and the lean body mass. Consequently, the correlation between wet mass of the whole butterfly and the contained lipid mass is weak and confounds the masses of water and lipid. In order to measure both accurately, the monarchs must be killed by freezing, weighed, dehydrated, weighed again, and then their lipids extracted and weighed (Brower *et al.* in prep.). Citizen-scientists could collect and freeze monarch samples and have professionals carry out the lipid and water determinations in a well-coordinated project.

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A REVIEW OF GEOGRAPHIC VARIATION AND POSSIBLE EVOLUTIONARY RELATIONSHIPS IN
THE *COLIAS SCUDDERII-GIGANTEA* COMPLEX OF NORTH AMERICA (PIERIDAE)

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ABSTRACT. The geographic variation in the *Colias scudderii-gigantea* complex of North America is reviewed. Transitional populations suggest that *C. gigantea* should be taxonomically treated within a broader polytypic concept of *C. scudderii*. Two of these transitional populations are described as new subspecies: *C. s. gracemina* in the Big Horn Mountains of Wyoming and *C. s. kohleri* in the mountains of western Montana. In addition, *C. s. nortepacifica*, new subspecies, is described from a remote region of southwestern British Columbia. Possible evolutionary relationships are examined with regard to the biogeography and paleohistorical climatic fluctuations and glaciations of the Pliocene-Pleistocene periods over the past seven million years. A phylogenetic hypothesis for the *chrysotheme* species group of *Colias* is presented that postulates reticulate hybrid fusion or introgression has played an important role in the evolution of this group of *Colias*.

Additional key words: Biogeography, phylogeny, glaciations, Pliocene, Pleistocene.

The genus *Colias* (Pieridae: Coliadinae) is a large and complex group of butterflies that is widely distributed throughout most of the world. Verhulst (2000) provided a monographic treatment of the genus, and recognized up to 85 species-level taxa. However, many of these taxa may be geographic subspecies or semispecies of complex polytypic species or superspecies (Hammond & McCorkle 2003). The genus is highly conservative in morphology with minimal genitalic differences among most of the species, with the exception of the subgenus *Zerene* (Verhulst 2000). Eleven major species groups may be distinguished within the genus on the basis of wing color pattern characters, including the subgenus *Zerene*. The latter group is often elevated to full generic status on the basis of morphological divergence.

Over the past twenty years, we have conducted extensive studies of species complexes closely related to *C. occidentalis* Scudder within the *chrysotheme* group of species. The present paper serves as an introduction to this group, and provides a detailed review of the *C. scudderii-gigantea* complex. Additional papers are planned that will review the *C. pelidnc-palaeno* complex and the *C. occidentalis-alexandra* complex. These complexes are of considerable interest from an evolutionary perspective. Evolutionary theory predicts that intermediate or transitional linkages should exist in modern day species complexes resulting from incipient speciation processes. As a consequence, the taxonomic delineation of species boundaries is often difficult for such intermediates. Such complexes may provide considerable evidence regarding the actual mechanical

processes of cladogenesis and speciation as they have taken place in the past, and may be taking place today.

As we define the *chrysotheme* species group, it consists of 11–15 species, depending upon interpretations of species boundaries. This group is confined to North America, with the exception of two species that are widespread in Eurasia. It is most similar and probably most closely related to the *crocea* species group in Eurasia and Africa, but differs in the absence of an androconial scale patch on the costal margin of the male dorsal hindwing. Other wing pattern characters that serve to distinguish most members of the *chrysotheme* group from the *crocea* group include (1) a lighter orange to yellow dorsal ground color, (2) reduced size of discal spots on fore and hindwings, and (3) a reduction or absence of heavy black melanic scaling on the dorsal hindwing of females. However, the Eurasian *C. chrysotheme* Esper tends to be intermediate in these latter characters between the North American species of the *chrysotheme* group and *C. crocea* Fourcroy.

Within the *chrysotheme* group, we recognize two subgroups based upon biology and some wing color pattern differences. The *chrysotheme* subgroup consists of the Eurasian *C. chrysotheme* and the North American species *C. eurytheme* Boisduval and *C. philodice* Godart. Together with *C. crocea*, these species are characterized on the ventral hindwing by having a double-ringed discal spot and black submarginal spots. Females always have fully developed black borders on the dorsal wings, and a

simple yellow-orange or white (alba) color dimorphism. All four species are highly vagile or even migratory. Their larvae feed on weedy legumes (Fabaceae) such as *Vicia*, *Trifolium*, and *Medicago* species that colonize disturbed and temporary habitats.

In sharp contrast, the *occidentalis* subgroup is usually characterized by having a single-ringed discal spot and reduced or absent black submarginal spots on the ventral hindwing. The black border of females is often reduced or completely absent. In addition, females also show an intermediate yellow-white or cream (semi-alba) color morph. These species are often very sedentary, and live in very local colonies in association with more stable habitats that support long-lived, perennial larval foodplants. The subgroup is comprised of three closely related species complexes that show numerous intermediate linkages. *Colias occidentalis* Scudder and *C. alexandra* Edwards form one complex that feeds on legumes, with *C. occidentalis* being possibly the primitive, ancestral species of the subgroup because of its close similarities with *C. philodice* and *C. eurytheme*. A more specialized, derived complex of species feed on *Vaccinium* shrubs (Ericaceae) growing in montane, boreal, and high Arctic habitats. These include the North American species *C. pelidne* Boisduval, *C. interior* Scudder, *C. behrii* Edwards, *C. chippewa* Edwards, and the Eurasian species *C. palaeno* Linnaeus. A third group that appears to be closely related to both *C. occidentalis* and *C. pelidne* is the *C. scudderii-gigantea* complex, feeding primarily on dwarf willows (*Salix* spp. – Salicaceae) growing in montane, boreal, or Arctic regions of North America. This species complex is the subject of the present paper.

Ferris (1987) has prepared the most recent monograph of the *C. scudderii-gigantea* complex. He recognized two separate species, *C. scudderii* Reakirt isolated in the southern Rocky Mountains, and *C. gigantea* Strecker distributed through the central and northern Rocky Mountains and across Canada and Alaska. However, other authors such as Scott (1986) have treated *C. gigantea* as a geographic subspecies of *C. scudderii*. In recent years, much additional information has been acquired from important geographic localities through the central Rocky Mountains. Four different intermediate populations show transitions from the typical Colorado *C. scudderii* to more northern populations of the *gigantea* type as discussed below. These are distributed in northeastern Utah, Wyoming, and southwestern Montana. Thus, we follow the taxonomic treatment of Scott (1986) in combining taxa of the *gigantea* type within a broader polytypic concept of *C. scudderii*.

MATERIALS AND METHODS

For this study, we examined about 1000 specimens of the *C. scudderii* complex from throughout the distribution of this species, but particularly from the Rocky Mountain region. In addition, we also examined about 900 specimens of *C. occidentalis* from across central Oregon to examine the relationship of this species to the *C. scudderii* complex.

Because of strong sexual dimorphism in this complex, males and females were studied separately. We measured forewing length from the wing base to the apex. We also quantified three wing color pattern characters in the male and two characters in the female. These characters all show continuous variation, and are probably controlled by polygenic complexes of multiple loci and alleles. However, for the purpose of this work, we wanted to simplify the analysis by reducing the variation classification to only a few classes. The characters and their classification are defined as follows.

1. Male ventral hindwing ground color olive-green, yellow-green, yellow, or orange. Since these colors present a situation of continuous variation and are probably highly polygenic, orange was classified as any tint of orange, ranging from very dark orange to pale yellow-orange. Likewise, olive-green was classified as darker shades without any yellow tinge, while yellow-green was classified as a paler green shade with a distinct tinge of yellow.

2. Male discal spot on ventral hindwing large, medium, or small. Spot size also shows a continuous range of variation, and was the most difficult to classify in an objective manner. A large spot was defined as covering one half or more of the discal cell width at the distal end of the cell, while a small spot covered only one third or less of discal cell width. A medium spot was subjectively treated as intermediate between these extremes. We also considered a subcategory of large spot called a giant spot that covers nearly two thirds of the discal cell width.

3. Male discal spot on ventral hindwing with or without a satellite spot.

4. Female dorsal ground color yellow, cream (semi-alba), white (alba), or orange. Again, orange was classified as any shade of orange including an orange flush on a yellow background.

5. Female black wing border on dorsal forewing heavy (both inner and outer parts of border present), reduced (usually only a thin portion of inner border present), or absent (only slight black traces of border present or none).

Tables 1 and 2 show the frequencies of polymorphic variants within these five characters in various

TABLE 1. Frequencies of phenotypic variation in males of *Colias scudderii* for ground color, discal spot size, and satellite spots on the ventral hindwing at various geographic localities.

Locality	olive-green	yellow-green	yellow	orange	large	medium	small	sat.	no sat.
1	0.79	0.21	0.00	0.00	0.25	0.30	0.45	0.27	0.73
2	1.00	0.00	0.00	0.00	0.33	0.33	0.33	0.50	0.50
3	0.26	0.74	0.00	0.00	0.55	0.25	0.20	0.84	0.16
4	0.25	0.25	0.50	0.00	0.65	0.27	0.08	0.75	0.25
5	0.00	0.00	0.69	0.31	0.54	0.23	0.23	0.81	0.19
6	0.00	0.01	0.67	0.32	0.46	0.26	0.28	0.73	0.27
7	0.04	0.24	0.63	0.09	0.50	0.28	0.22	0.82	0.18
8	0.00	0.00	0.60	0.40	0.43	0.37	0.20	0.83	0.17
9	0.00	0.00	0.28	0.72	0.38	0.28	0.34	0.66	0.34
10	0.00	0.00	0.58	0.42	0.37	0.32	0.31	0.89	0.11
11	0.00	0.00	0.50	0.50	0.25	0.33	0.42	0.92	0.08
12	0.05	0.05	0.40	0.50	0.35	0.45	0.20	0.80	0.20

1. Colorado, Rocky Mts. n = 108 (*C. s. scudderii*)
2. Utah, Uinta Mts. n = 6 (*C. s. scudderii* Uinta population)
3. Wyoming, Big Horn Mts. n = 73 (*C. s. gracemina*)
4. Wyoming, Wind River Mts. n = 55 (*C. s. harroweri*)
5. Wyoming, Absaroka Mts. n = 26 (*C. s. kohleri*)
6. Montana, Centennial Mts. n = 95 (*C. s. kohleri*)
7. Montana, Pioneer Mts. n = 147 (*C. s. kohleri*)
8. Montana, Flint Creek Mts. n = 35 (*C. s. kohleri*)
9. Alberta and British Columbia n = 29 (*C. s. mayi*)
10. Manitoba, Riding Mts. n = 19 (*C. s. mayi*)
11. Manitoba, Hudson Bay at Churchill n = 12 (*C. s. gigantea*)
12. Yukon and Alaska n = 20 (*C. s. gigantea*)

populations of the *C. scudderii* complex at strategic locations across the North American landscape. We attempted to assemble a minimum sample of 10 specimens for each population to show at least the major variations within these populations, although 15–20 specimens provides better insight into frequencies. The larger samples of 50 or more were useful for detecting rare variants in populations. It should be noted that these are composite samples comprised of individuals from many localities, and do not represent single or local colonies.

RESULTS AND DISCUSSION

***Colias occidentalis* and possible evolutionary relationships.** Relationships among the various *Colias* species in western North America have been very confused in the past. This is due to the existence of numerous intermediate or transitional populations, not only within species complexes, but also between complexes. Hybridization also appears to be an important evolutionary process in these butterflies. As a consequence, applying the taxonomic definition of

species has been very difficult, often arbitrary, and artificial. We are using the biological species concept based upon reproductive isolation in sympatry, but even this concept is often inadequate for the taxonomic delineation of species boundaries. Nevertheless, the various intermediate or transitional populations that exist in the modern day provide much evidence regarding the past evolutionary history of the butterflies, and are the basis for the following evolutionary theories.

Ferris (1993) conducted a cladistic analysis of the group, and recognized five species feeding on legumes within the *occidentalis* subgroup. The typical form of *C. occidentalis* along the West Coast is yellow with no UV-reflectance. It is extremely similar to *C. philodice eriphyle* Edwards in most characteristics, particularly those *C. occidentalis* populations in southwest Oregon and northwest California. The primary differences between the two species are that *C. occidentalis* has a single-ringed discal spot and heavier black melanic scaling on the ventral hindwing. By contrast, populations in the central and northern Rocky Mountains and across central Canada are more

TABLE 2. Frequencies of phenotypic variation in females of *Colias* for dorsal ground color and development of the black wing border at various geographic localities.

Locality	white	cream	yellow	orange	heavy	reduced	absent
1	0.50	0.19	0.31	0.00	0.03	0.19	0.78
2	0.60	0.20	0.20	0.00	0.00	0.00	1.00
3	0.30	0.38	0.30	0.02	0.18	0.32	0.50
4	0.05	0.10	0.76	0.09	0.09	0.57	0.34
5	0.08	0.33	0.58	0.00	0.42	0.17	0.41
6	0.22	0.17	0.61	0.00	0.39	0.39	0.22
7	0.19	0.10	0.70	0.01	0.09	0.20	0.71
8	0.00	0.00	0.88	0.12	0.18	0.41	0.41
9	0.00	0.14	0.86	0.00	0.14	0.29	0.57
10	0.67	0.33	0.00	0.00	0.00	0.50	0.50
11	0.70	0.30	0.00	0.00	0.30	0.40	0.30

1.	Colorado, Rocky Mts. n = 32 (<i>C. s. scudderii</i>)
2.	Utah, Uinta Mts. n = 5 (<i>C. scudderii</i> Uinta population)
3.	Wyoming, Big Horn Mts. n = 40 (<i>C. s. gracemna</i>)
4.	Wyoming, Wind River Mts. n = 21 (<i>C. s. harroweri</i>)
5.	Wyoming, Absaroka Mts. n = 12 (<i>C. s. kohleri</i>)
6.	Montana, Centennial Mts. n = 23 (<i>C. s. kohleri</i>)
7.	Montana, Pioneer Mts. n = 87 (<i>C. s. kohleri</i>)
8.	Alberta and British Columbia n = 17 (<i>C. s. mayi</i>)
9.	Manitoba, Riding Mts. n = 7 (<i>C. s. mayi</i>)
10.	Manitoba, Hudson Bay at Churchill n = 6 (<i>C. s. gigantea</i>)
11.	Yukon and Alaska n = 10 (<i>C. s. gigantea</i>)

divergent with orange dorsal color and UV-reflectance on both fore and hindwings of males. Ferris (1993) recognized these populations as three taxonomic species, *C. christina* Edwards, *C. pseudochristina* Ferris, and *C. krauthii* Klots. The fifth legume feeder is *C. alexandra*, which is mostly yellow with a UV-reflecting patch on the dorsal hindwing. Finally, Ferris (1987) also reported *C. gigantea* from central Oregon.

Warren (2005) has followed Ferris (1993) in treating *C. christina* as distinct from *C. occidentalis*. However, as discussed by Hammond & McCorkle (2003), a long clinal gradient between yellow *occidentalis* forms and orange *christina* forms exists across the entire Intermountain region between the Cascades and Rocky Mountains. We examined long series of specimens from many localities. The Cascade populations are nearly monomorphic yellow, but one orange specimen was found in Jefferson County, Oregon at the closest geographic point between the Cascades and the Ochoco Mountains to the east. This gives a ratio of about 99% yellow and 1% orange for the Jefferson County population. Eastward, we found the yellow:orange ratio to be about 90:10 in the Ochoco Mountains, 70:30 in the Aldrich Mountains, 50:50 in the central Blue

Mountains, 30:70 in the northern Blue Mountains, 10:90 in the Wallowa Mountains, and 5:95 in central Idaho. We also found that up to 12% of specimens from the east slope of the Rocky Mountains in Alberta are mostly yellow with only a slight orange flush, and that the frequency of yellow or near yellow butterflies increases southward in Montana (see Kohler, 2006). Because of these long, gradual clines between yellow and orange morphs, we suggested that the *christina* group should be taxonomically treated as subspecies of *C. occidentalis*. Throughout the Great Basin and Intermountain regions, *C. occidentalis* feeds primarily on legumes such as peas (*Lathyrus* spp.) and false lupines (*Thermopsis* spp.). In sharp contrast, *C. alexandra* functions as a fully distinct biological species in these same regions, and specializes on highly toxic legumes such as milk-vetches (*Astragalus* spp.) and locoweeds (*Oxytropis* spp.).

Although Ferris (1987) reported *C. gigantea* from central Oregon, no actual populations have ever been found and verified. However, while we were examining some 900 specimens of *C. occidentalis* across central Oregon to study the yellow-orange cline discussed above, we observed large numbers of specimens that

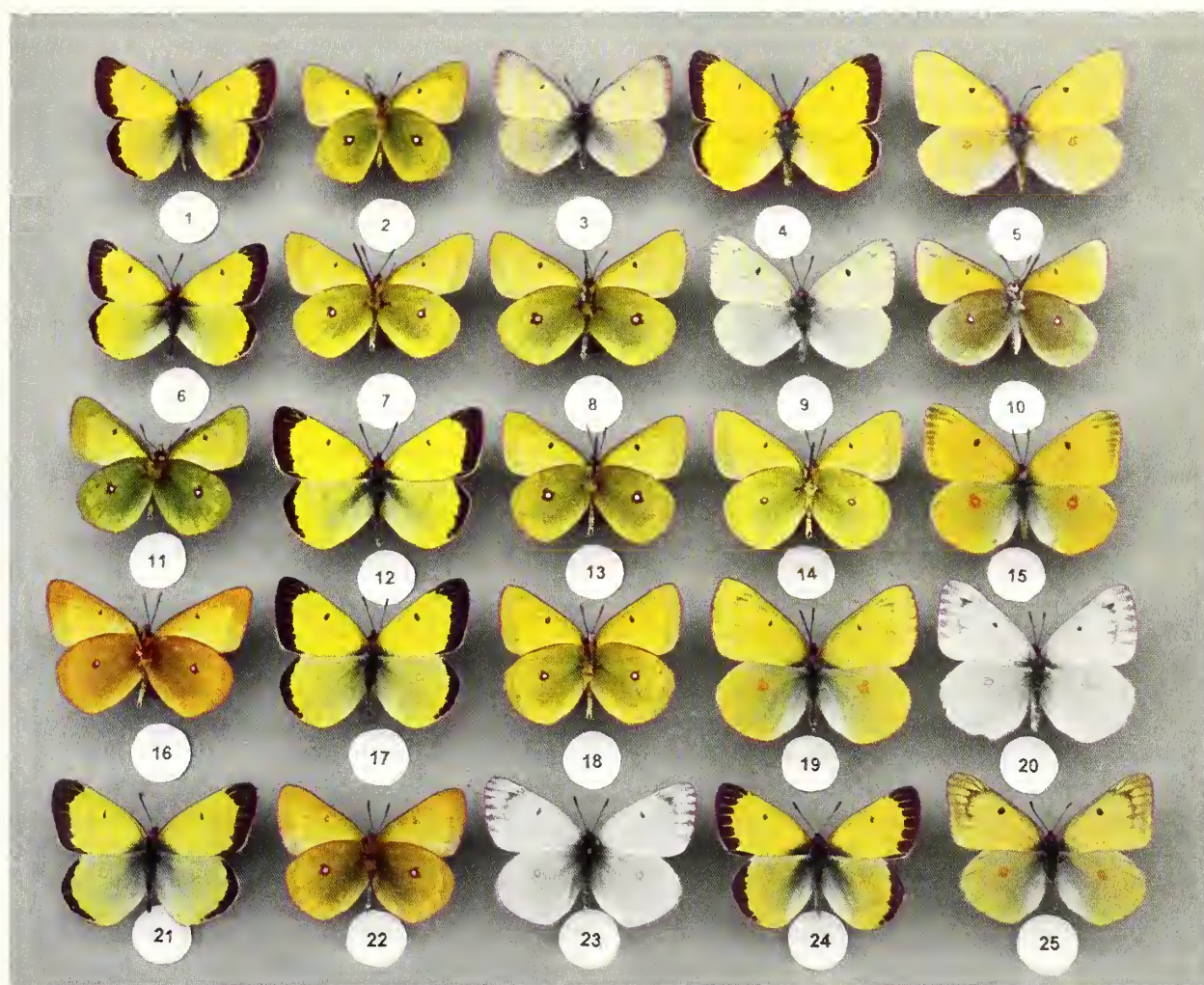


FIG. 1. (1) *Colias scudderii scudderii*, male dorsal, Colorado; (2) *C. s. scudderii*, male ventral with giant discal spots, Colorado; (3) *C. s. scudderii*, female dorsal cream form, Colorado; (4) *C. s. mayi*, male dorsal, Manitoba; (5) *C. s. mayi*, female dorsal yellow form, Manitoba; (6) *C. s. gracinnna*, Holotype male dorsal, Wyoming; (7) *C. s. gracinnna*, male ventral yellow-green form with medium discal spots, Wyoming; (8) *C. s. gracinnna*, male ventral with giant discal spots, Wyoming; (9) *C. s. gracinnna*, Allotype female dorsal cream form, Wyoming; (10) *C. s. gracinnna*, female ventral with bicolored hindwing, Wyoming; (11) *C. s. gracinnna*, male ventral olive-green *scudderii*-like form, Wyoming; (12) *C. s. harroweri*, male dorsal, Wyoming; (13) *C. s. harroweri*, male ventral olive-green form with giant discal spots, Wyoming; (14) *C. s. harroweri*, male ventral yellow form with small discal spots, Wyoming; (15) *C. s. harroweri*, female dorsal orange form, Wyoming; (16) *C. s. mayi*, male ventral dark orange form with small discal spots, Alberta; (17) *C. s. kohleri*, Holotype male dorsal, Montana; (18) *C. s. kohleri*, male ventral yellow-orange form with medium discal spots, Montana; (19) *C. s. kohleri*, Allotype female dorsal yellow form, Montana; (20) *C. s. kohleri*, female dorsal white form, Montana; (21) *C. s. gigantea*, male dorsal, Alaska; (22) *C. s. gigantea*, male ventral orange form with large discal spots, Alaska; (23) *C. s. gigantea*, female dorsal white form, Alaska; (24) *C. s. nortepacifica*, Holotype male dorsal, British Columbia; (25) *C. s. nortepacifica*, Allotype female dorsal, British Columbia.

had a phenotype virtually identical to that of *C. gigantea*, and this phenotype appears to be the basis for Ferris' report. Moreover, we also observed extreme phenotypes within these samples that were virtually identical to those of *C. scudderii* in the southern Rocky Mountains and *C. pelidne skinneri* Barnes in the central and northern Rocky Mountains. All of the *Vaccinium-Salix* feeding species of *Colias* are yellow in the males with no UV-reflectance like the West Coast forms of *C. occidentalis*. The existence of these intermediate

populations in central Oregon and the intermediate populations discussed below provide much evidence for evolutionary linkages among all three species complexes.

The above observations have suggested to us a possible theory of genealogy and evolutionary history for the *chrysotheme* species group. Based upon the cladistic analysis, a simple linear genealogy for the *chrysotheme* subgroup appears to exist across Eurasia and North America beginning with *C. crocea* in

southern Eurasia. Evolutionary steps in this genealogical sequence are (1) loss of the male androconical patch in *C. chrysotheme* in northern Eurasia, (2) reduction in discal spot size and black melanic scaling in *C. eurytheme* in North America, (3) loss of orange coloration and UV-reflectance in *C. philodice*, and (4) loss of the double-ringed discal spot and black submarginal spots in West Coast forms of *C. occidentalis*.

At this point, evolutionary patterns in the *occidentalis* subgroup become very complicated. While the linear genealogy of the *chrysotheme* subgroup could be viewed in a traditional dichotomous hierarchy of a standard cladistic analysis, the *occidentalis* subgroup genealogy appears to be a multibranching or polychotomous pattern quite unlike the cladogram presented by Ferris (1993). Also, reticulate hybrid fusion or introgression appears to have played an important role in the evolution of this group of *Colias*.

An important theoretical concept is that of punctuated equilibrium (Gould & Eldredge 1977), the idea that taxa or populations are distributed through time as well as space, and share ancestor-descendant relationships as a consequence (see discussion in Hammond 1991). Such relationships are never evident in a cladistic analysis with a nested dichotomous hierarchy. Instead, ancestral taxa are thought to produce large numbers of descendant taxa during an adaptive radiation in a multibranching or polychotomous pattern, while surviving largely intact and largely unchanged through long periods of time, often as relicts in more restricted and isolated refugia. Thus, *C. occidentalis* is postulated to be the immediate ancestral parent species for three distinct daughter species; *C. pelidne*, *C. scudderii*, and *C. alexandra*.

Based upon our analysis of phenotypic variation in central Oregon populations of *C. occidentalis*, and the other intermediate populations discussed below, we suggest that both *C. scudderii* in the southern Rocky Mountains and *C. pelidne* in the central and northern Rocky Mountains represent geographic isolates of ancestral *C. occidentalis* populations from the Intermountain region. Such isolation events may have taken place in the late Miocene or Pliocene about 4–7 million years ago as conditions in the Rocky Mountains became cooler leading up to the glacial and interglacial periods of the Pleistocene. Such climatic shifts may have promoted a foodplant shift in Rocky Mountain populations away from legumes such as *Lathyrus* in favor of *Salix* and *Vaccinium* shrubs in subalpine environments.

Later during the Pleistocene, as *C. scudderii* spread northward through the central Rocky Mountains of

Wyoming and Montana and into Canada and Alaska, *C. occidentalis* also spread into this region, initially hybridizing with *C. scudderii* to produce the modern *gigantea* phenotype. Eventually, Rocky Mountain populations of *C. o. christina* acquired full reproductive isolation from *C. scudderii*. The orange color and UV-reflectance of *C. o. christina* may represent characters that were acquired in the Intermountain and northern Rocky Mountain regions from hybridization with *C. eurytheme* and *C. meadii* Edwards, and these characters were strongly selective in the northern Rocky Mountains and across Canada as a way to reproductively isolate *C. o. christina* from *C. scudderii* (Ferris 1993).

Still later, *C. o. christina* spread southward through the central Rocky Mountains of Montana and Wyoming, and into the southern Rocky Mountains of Colorado to speciate into the modern *C. alexandra*, where it ecologically replaces *C. occidentalis*. The further adaptive radiation of *C. alexandra* populations throughout the western Great Plains, Great Basin, and Intermountain regions appears to be of relatively recent origin, a response to the climatic drying and desertification of these regions during the Pleistocene that resulted in a large adaptive radiation of the legume genus *Astragalus* (Isely 1983).

We realize that the above evolutionary scenarios are highly speculative, but the existence of modern intermediate populations provides important supportive evidence. Such hypotheses are potentially testable as additional evidence becomes available in the future, perhaps using molecular markers. Also, this theory serves as a background context for discussing the patterns of geographic variation and ecology within the *C. scudderii* complex below.

Subspecies Descriptions

Colias scudderii ruckesi Klots

The taxonomic status of this subspecies is somewhat confused. Klots (1937) described this taxon from the south end of the Sangre de Cristo Range in the Pecos River drainage near Santa Fe, New Mexico. The type series was collected in 1935 and 1936. According to Klots' description, this subspecies is distinctly different from the typical *C. s. scudderii* in Colorado and Wyoming. Diagnostic characters cited by Klots for *C. s. ruckesi* include (1) larger size, (2) reduction or absence of the black discal spot on the dorsal forewing, (3) a broader black marginal border in the male, (4) a deeper yellow dorsal ground color, (5) heavier and more extensive black basal suffusion, and (6) a higher frequency of the yellow morph in females.

However, Ferris (1987) collected specimens of *C. s. ruckesi* from the type locality later in the 1970's, and was

not able to distinguish these from typical *C. s. scudderii* in Colorado. It is possible that warmer climatic conditions during the 1930's may have influenced the phenotype, producing larger and darker colored butterflies compared to the 1970's. We have only examined two specimens of *C. s. ruckesi*, and have no new information to contribute regarding this question. In general, peripheral isolates such as *C. s. ruckesi* often exhibit some divergence, at least in gene and phenotype frequencies, compared to more centrally located populations.

Colias scudderii scudderii Reakirt

Figure 1, Tables 1 & 2

Description. Male (n=108). Forewing length 22–25 mm, mean = 24 mm. Dorsal ground color pale yellow. Black border of forewing usually broad, sometimes narrow, with yellow veins. Small black discal spot of forewing usually prominent or reduced, rarely absent. Moderate to heavy black basal suffusion present on fore and hindwings. Discal spot on dorsal hindwing usually yellow and faint. Black scaling in medial area of ventral forewing light to absent. Ventral ground color of hindwing usually olive-green (79%), sometimes yellow-green (21%) with heavy black melanic scaling. Discal spot on ventral hindwing ringed with red, variably large (22%), medium (33%), or small (45%). A satellite spot is usually absent (73%), sometimes present (27%).

Female (n=32). Forewing length 23–26 mm, mean = 25 mm. Dorsal ground color variable, white (52%), cream (19%), or yellow (29%). Black border of dorsal forewing is usually completely absent (78%), sometimes partially present (19%), and rarely fully developed (3%). Discal spot of dorsal hindwing usually yellow and faint, rarely orange. Ground color of ventral hindwing variable, usually olive-green to yellow-green, sometimes orange. Other characters as in male.

Distribution and ecology. This subspecies is common and widely distributed throughout the southern Rocky Mountains of Colorado, extending northward through the Medicine Bow and Laramie Mountains of southeastern Wyoming in Carbon, Albany, and Converse Counties. However, populations in the Sangre de Cristo Range of south-central Colorado extending southward through northern New Mexico are tentatively assigned to *C. s. ruckesi* as discussed above.

The habitat used by *C. s. scudderii* is more variable and extends over a much broader elevational gradient than suggested by Ferris (1987). The butterfly occupies open forests of quaking aspen and conifers or open meadows within the forest at middle elevations, and subalpine or alpine meadows at high elevations at or above timberline. The high elevation populations appear to be feeding mostly on dwarf willows (*Salix* spp.) as larval foodplants, but there are also numerous records of oviposition on *Vaccinium caespitosum* Michx. in Colorado (Scott 1986; Ferris 1987).

We have also observed oviposition on *Lathyrus lanszwertii* var. *leucanthus* Rydb. in Colorado. One of us (PCH) found *C. scudderii* to be common at middle elevations on the west side of Gore Pass in Routt

County during 1996. A large clear-cut was made in a dry, upland mixed forest of quaking aspen and lodgepole pine. *Lathyrus lanszwertii* had densely colonized this open clear-cut, and was a major part of the ground cover. A large colony of about 30–40 adults of *C. scudderii* was flying in this clear-cut, and at least three different females were observed ovipositing on the *Lathyrus* together with females of *C. alexandra*.

Discussion. *Colias s. scudderii* appears to be a highly specialized subspecies at least in morphology. The very small wing length combined with the monomorphic olive-green to yellow-green ground color on the ventral hindwing of males are strong diagnostic characters for this subspecies. In addition, it shows a high frequency of a small discal spot combined with no satellite spot on the ventral hindwing. In females, about 70% are white or cream in dorsal ground color and only about 30% are yellow. The black wing border in females is usually absent or greatly reduced.

In spite of these specializations, the subspecies appears to be quite generalized in ecology with polyphagous larvae, feeding on *Salix*, *Vaccinium*, and *Lathyrus*. In sharp contrast, three distinct species co-exist together in sympatry within the central and northern Rocky Mountains, with other *C. scudderii* subspecies using *Salix* exclusively as a larval foodplant, *C. pelidne* using *Vaccinium*, and *C. occidentalis* or *C. alexandra* using legumes such as *Lathyrus*. Thus, in Colorado, *C. s. scudderii* appears to be fully or partially using the foodplant niches of three different species in the central and northern Rocky Mountains, although the *Lathyrus* niche is mostly occupied by *C. alexandra* in much of Colorado (Hayes 1980).

As previously discussed, *C. s. scudderii* appears to be a sister species of *C. pelidne*, and both appear to have been isolated in the southern and north-central Rocky Mountains respectively from Intermountain ancestral populations of *C. occidentalis*. Both switched away from the ancestral *Lathyrus* foodplants in favor of *Salix* and *Vaccinium* foodplants as climatic conditions became cooler in the Rocky Mountains prior to the Pleistocene glaciations. While isolated in the southern Rocky Mountains, *C. s. scudderii* has retained this evolutionary transition into modern times using diverse and multiple larval foodplants, while sympatric northern populations have evolved very narrow foodplant specializations as part of their speciation processes.

Colias scudderii Uinta Range population

An isolated population of *C. scudderii* occurs at high elevations in the Uinta Range of northeast Utah, including Summit, Daggett, Duchesne, and Uintah Counties. We have only examined a short series of 6

males and 5 females from this population (Tables 1 & 2). Most of these specimens are very similar to the Colorado *C. s. scudderii* in phenotype, but one male and one female are larger and similar in phenotype to the Wyoming *C. s. harroweri* Klots. We believe this population is transitional between the two subspecies.

Jacque Wolfe and Jack Harry (per. comm.) have made extensive ecological observations of the Uinta Range population. Most females oviposit on low *Vaccinium* species such as *V. caespitosum* growing in open conifer forests at high elevations. However, Jack Harry (per. comm.) also observed a local colony in a riparian zone along a creek where females were ovipositing on a tall *Salix* species. Thus, the Uinta Range population appears to retain polyphagous feeding habits like the Colorado populations.

In ecology, this population is intermediate between Colorado *C. scudderii* and Wyoming *C. pelidne skinneri*, and is mostly occupying the ecological niche of *C. pelidne* in the Uinta Range. However in morphology, the population appears to be intermediate between Colorado *C. s. scudderii* and Wyoming *C. s. harroweri*.

***Colias scudderii gracemma* Hammond &**

McCorckle, new subspecies

Figure 1, Tables 1 & 2

Description. **Male** (n=73). Wings often elongate. Forewing length 22–27 mm, mean = 25 mm. Dorsal ground color pale yellow. Black border of forewing variably broad to narrow with yellow veins. Small black discal spot of forewing oblong, prominent, rarely faint or absent. Moderate to heavy black basal suffusion present on fore and hindwings. Discal spot on dorsal hindwing usually yellow and faint, rarely pale orange. Black scaling in medial area of ventral forewing light to absent. Ventral ground color of hindwing usually bright yellow-green (74%), sometimes darker olive-green (26%), with heavy black melanic scaling. Discal spot on ventral hindwing ringed with red, variably large (55%), medium (25%), or small (20%). A satellite spot is usually present (84%), rarely absent (16%).

Female (n=40). Forewing length 24–28 mm, mean = 26 mm. Dorsal ground color variable, white (30%), cream (38%), yellow (30%), or rarely with an orange flush (2%). Black border of dorsal forewing is usually completely absent (50%) or partially present (32%), and sometimes fully developed (18%). Discal spot of dorsal hindwing variably pale yellow to orange. Ground color of ventral hindwing blue-green to yellow-green, or bicolored darker orange in the medial portion of the wing with a paler blue-green submarginal band. Other characters as in the male.

Holotype. male, Wyoming, Johnson County, summit of Big Horn Mountains near Cloud Peak Wilderness Area, 13 July 2004, Terry Stoddard leg. The holotype is deposited in the Oregon State Arthropod Collection, Oregon State University, Corvallis, Oregon, USA. **Allotype.** female, same data and deposition as holotype, but collected 19 July 2005. **Paratypes.** 65 males and 33 females, same locality as holotype. Disposition of paratypes as follows: 41 males and 20 females to the collection of Terry Stoddard, 18 males and 8 females to the collection of Steve Van Campen, and 6 males and 5 females to the collection of Paul C. Hammond.

Etymology. The name honors Grace Stoddard and Emma Van Campen who helped collect and study this butterfly.

Distribution and ecology. This subspecies is narrowly endemic to the Big Horn Mountains in Wyoming, and is presently known only from the south end of the mountains in Johnson County near the Cloud Peak Wilderness Area. It occurs in broad, extensive willow bogs or meadows at high elevations near the summit of the mountains. Females have been observed ovipositing on a low-growing dwarf willow (*Salix* sp.) in these bogs. At somewhat lower elevations in the Big Horn Mountains, there are extensive willow bogs dominated by a different species of willow that grows much taller into a large bush or small tree. *Colias s. gracemma* was never found in association with this tall willow, and is very habitat limited as a consequence. Within the meadow and adjacent forest habitats, this species is sympatric with three other species of *Colias* including *C. pelidne skinneri*, *C. occidentalis sacajawea* Kohler, and *C. philodice*.

Diagnosis and discussion. This population is a distinctive isolate that is exactly intermediate between the Colorado *C. s. scudderii* and the more *gigantea*-like populations to the north. Although Ferris (1987) knew of this population, he may not have seen sufficient material to recognize the following unique characteristics. Characters shared with *C. s. scudderii* include (1) males that are monomorphic green on the ventral hindwing, (2) females that are commonly white or cream (68%) in dorsal ground color, and (3) females in which the black wing border is mostly reduced or completely absent (82%). Characters shared with *gigantea*-like forms include (1) a high frequency of a large discal spot on the ventral hindwing (55%), and (2) a high frequency of a satellite spot (84%). In size, *C. s. gracemma* is also intermediate between the southern and central Rocky Mountain subspecies of *C. scudderii*. Moreover, it should also be noted that extreme specimens of *C. s. gracemma* are virtually identical in phenotype to either the Colorado *C. s. scudderii* or the western Wyoming *C. s. harroweri* Klots.

This subspecies does exhibit several unique features not found commonly in the other subspecies. The wings are quite elongate compared to most other subspecies. Males usually have a bright or vivid yellow-green ground color on the ventral hindwing, in contrast to the darker olive-green ground color common in Colorado *C. s. scudderii*. Females frequently are bicolored on the ventral hindwing, with an orange medial area contrasting with a paler blue-green submarginal area. Females in other subspecies of *C. scudderii* also frequently show a darker, more brownish medial area on the ventral hindwing, as do rare females of *C. pelidne* and *C. occidentalis*, but these are rarely as contrasting as are the colors in some females of *C. s. gracemma*.

We suggest that *C. s. gracemma* represents a peripheral isolate of *C. scudderii* populations that spread northward out of Colorado during early Pleistocene glaciations, initially hybridizing with ancestral populations of *C. occidentalis* to the north that produced the modern *gigantea*-like phenotypes in northern populations.

Colias scudderii harroweri Klots

Figure 1, Tables 1 & 2

Description. Male (n=55). Forewing length 23–28 mm, mean = 26 mm. Dorsal ground color pale yellow. Black border of forewing variable, narrow to broad, with yellow veins. Black discal spot of forewing variable, small and faint to large and round. Moderate to heavy black basal suffusion present on fore and hindwings. Discal spot on dorsal hindwing faint yellow to orange. Black sealing in medial area of ventral forewing usually absent. Ventral ground color of hindwing variable olive-green (25%), yellow-green (25%), or yellow (50%) with light to heavy black melanic scaling. Discal spot on ventral hindwing ringed with red, usually large to giant (65%), sometimes medium (27%), or rarely small (8%). A satellite spot is usually present (75%), sometimes absent (25%).

Female (n=21). Forewing length 26–29 mm, mean = 27 mm. Dorsal ground color usually yellow (76%), rarely white (5%), cream (10%), or orange (9%). Black border of dorsal forewing is usually absent (34%) or partially present (57%), rarely fully developed (9%). Discal spot of dorsal hindwing usually faint orange to dark orange. Ground color of ventral hindwing yellow to blue-green. Other characters as in male.

Distribution and ecology. This subspecies is narrowly endemic to the mountains of western Wyoming in the Teton and Wind River Ranges of Teton, Sublette, and Fremont Counties. As we narrowly define this taxon, it does not occur in the Yellowstone region of Wyoming and Montana, but is replaced northward by subspecies discussed below.

The butterfly is found in a variety of willow bog habitats at middle to high elevations in the mountains. These include riparian bogs along forest streams, extensive seepage areas in semi-open lodgepole pine forests, and extensive hanging bog meadows. Females oviposit on a dwarf willow species (*Salix* sp.) in these bogs. This species is sympatric in the Wind River Range with *C. pelidne*, *C. alexandra astraea* Edwards, and *C. philodice*.

Discussion. This is the third subspecies or population that appears to be intermediate between the Colorado *C. s. scudderii* and the more *gigantea*-like populations to the north. However, unlike the *C. s. gracemma* populations to the east in the Big Horn Mountains, these western populations appear to be more directly intergrading between *C. s. scudderii* and *C. s. kohleri* (described below) in Montana. Transitional characters include larger size, a mixture of green and yellow ground colors on the ventral hindwing of males, and a high frequency of the yellow morph in females. However, extreme specimens are still identical in phenotype to the Colorado *C. s. scudderii*, particularly

at the south end of the Wind River Range in Fremont County.

One character that uniquely distinguishes *C. s. harroweri* is a high frequency of a giant discal spot on the ventral hindwing. This extreme character occurs in many populations of *C. occidentalis* and *C. pelidne*, but is usually quite rare (1–5%).

In *C. s. scudderii*, the frequency of giant spots is 12%, and is 23–31% in most other populations of *C. scudderii* throughout North America. However, this character reaches the highest frequency in *C. s. harroweri* at 50%, compared to a frequency of 27% in *C. s. gracemma*.

Colias scudderii kohleri Hammond & McCorkle, new subspecies

Figure 1, Tables 1 & 2

Description. Male (n=360). Forewing length 25–29 mm, mean = 27 mm. Dorsal ground color variable, pale to dark yellow, usually medium yellow. Black border of forewing usually broad, rarely narrow, with yellow veins. Black discal spot of forewing often large and prominent, round to oblong, rarely faint or absent. Black basal suffusion on fore and hindwings usually moderate to reduced, sometimes heavy. Discal spot on dorsal hindwing pale yellow to orange. Black scaling in medial area of ventral forewing usually absent to light, rarely moderate. Ventral ground color of hindwing variable, usually yellow or orange, sometimes green. Black melanic scaling on ventral hindwing usually moderate to heavy, sometimes reduced. Discal spot on ventral hindwing ringed with red, variably large (43–54%), medium (23–37%), or small (20–28%). A satellite spot is usually present (73–83%), sometimes absent (17–27%).

Female (n=180). Forewing length 26–30 mm, mean = 28 mm. Dorsal ground color variable, usually yellow (58–70%), sometimes white (8–22%), or cream (10–33%), rarely orange (1%). Black border of dorsal forewing variable, poorly developed in some populations, well developed in other populations. Discal spot of dorsal hindwing variably pale to dark orange. Ground color of ventral hindwing variably yellow, orange, or blue-green. Other characters as in the male.

Holotype. male, Montana, Beaverhead County, summit of the Pioneer Mountains, 21 July 2002, Paul C. Hammond leg. The holotype is deposited in the Oregon State Arthropod Collection, Oregon State University, Corvallis, Oregon, USA. **Allotype.** female, same data and deposition as holotype. **Paratypes.** 93 males and 50 females, same locality as holotype. Disposition of paratypes as follows: 13 males and 16 females to the collection of Terry Stoddard, 45 males and 8 females to the collection of Steve Van Campen, 8 males and 7 females to the collection of Steve Kohler, 5 males and 4 females to the collection of David V. McCorkle, and 22 males and 15 females to the collection of Paul C. Hammond.

Etymology. The name honors Steve Kohler, who has made an immense contribution to the study of Montana butterflies.

Distribution and ecology. This subspecies as we define it here is widely distributed in the central Rocky Mountain region, from the greater Yellowstone ecoregion in northwest Wyoming north throughout most of western Montana to Flathead County, and west to the west slope of the Bitterroot Range in Lemhi County, Idaho. Ferris (1987) has reported a record from Blaine County in south-central Idaho, but we have not been able to verify this record. Earlier reports

(Ferris 1987) from central Oregon are probably misidentified *C. occidentalis*.

This subspecies occupies extensive, open boggy meadows with dwarf willows, either at middle elevations in hanging bogs on mountain slopes and in riparian zones along creeks, or in subalpine meadows at the higher elevations in the mountains. At the type locality in the Pioneer Mountains, there are actually two distinct species of dwarf willows growing together in sympatry; one with green leaf petioles and hairy leaves, and one with red petioles and smooth leaves. The females of *C. s. kohleri* at this locality were highly selective in their choice for oviposition, and were observed to oviposit only on the red petiole-smooth leaf type of willow. This *Salix* might be either *S. boothii* Dorn or *S. planifolia* Pursh.

Diagnosis and discussion. This subspecies is extremely similar in phenotype to common forms of *C. occidentalis* across central Oregon. In fact, we know of no diagnostic character that consistently separates the two species. On average, males of *C. s. kohleri* show reduced black basal suffusion on the dorsal wings compared to males of *C. occidentalis*, but there is much overlap between them. Also, *C. s. kohleri* shows a much higher frequency of giant discal spots on the ventral hindwing (23–36%) compared to *C. occidentalis* (1–5%).

There is a slight average difference between the two species in the wing pattern of females on the dorsal forewing. In females with partial or full development of the black wing border, *C. scudderii* usually exhibits a stronger development of the inner portion of the border that appears as a thin, black line, while the outer portion is often obscure or completely absent. This development is most often exactly reversed in females of *C. occidentalis*. Again, however, this character is not consistently different between the two species, and immaulate females are essentially identical.

We suggest that *C. s. scudderii* spread northward out of Colorado during early glacial periods of the Pleistocene, eventually hybridizing with ancestral populations of *C. occidentalis* in the central Rocky Mountains of Montana. This reticulate hybrid fusion resulted in the modern *gigantea*-like phenotype of *C. s. kohleri* that closely resembles the ancestral phenotype of *C. occidentalis*, but retains the specialized larval feeding niche on dwarf willows of the *C. s. scudderii* parent. Eventually, reproductive isolation between the two species was attained, perhaps with help from the orange-UV coloration acquired later by *C. occidentalis* males in the central-northern Rocky Mountain region. Foodplant incompatibility between the legume-feeding and willow-feeding niches was probably the driving selective force that promoted eventual reproductive

isolation and full speciation.

There is some geographic variation in populations of *C. s. kohleri* that is probably of evolutionary significance. The most variable populations are found at the type locality in the Pioneer Mountains of Beaverhead and Deer Lodge Counties, Montana (Tables 1 & 2). Consequently, this region is thought to be the historical center of origin for the original hybridization between *C. scudderii* and *C. occidentalis*, and the original point of origin for *C. s. kohleri*. These populations still exhibit a relatively high frequency of *scudderii*-like green colors on the ventral hindwing of males, 24% yellow-green and even 4% olive-green. Also, females are mostly immaulate (71%), and only about 29% show partial or full development of the black wing border.

In sharp contrast, the populations of *C. s. kohleri* in the greater Yellowstone ecoregion are highly divergent from the original *scudderii*-like phenotype (Tables 1 & 2), even though they are geographically closest to the *scudderii*-like *C. s. gracemma* and *C. s. harroweri* populations in Wyoming. Both the Absaroka Range population in Park County, Wyoming and the Centennial Range population in southern Beaverhead County, Montana and adjacent Fremont County, Idaho are almost monomorphic for yellow or orange colors on the ventral hindwing of males (99–100%), and very rarely show green colors (1%) of the *scudderii* type. Also, females show a much higher frequency of partial or full development of the black wing border (59–78%). For these reasons, we believe the Yellowstone region populations are of relatively recent origin, possibly spreading into this region since the last Pleistocene glaciation. They appear to have had little genetic contact with the older *C. s. harroweri* populations to the south in the Teton region.

Northward from the Pioneer Mountains, populations of *C. s. kohleri* also show reduced variation, and are mostly monomorphic yellow or orange on the ventral hindwing in Granite, Missoula, Lake, and Flathead Counties. We have seen only a few specimens from the east slope of the Rocky Mountains in northern Montana, but these closely resemble the Canadian *C. s. mayi* Chermock. A population in Lewis and Clark County appears to be intermediate between *C. s. kohleri* and *C. s. mayi*, but the population in Glacier County belongs to this Canadian subspecies.

During later periods of the Pleistocene, *C. s. kohleri* appears to have produced four distinct evolutionary lineages of the *gigantea*-type in Canada and Alaska. These include the following *C. s. mayi* to the northeast in central Canada, *C. s. gigantea* Streecker in the subarctic north, *C. s. inupiat* Harry in the far arctic north of Alaska, and an unnamed segregate in the northwest.

The evolutionary history of these four northern segregates appears to be intimately connected with the history of Pleistocene glacial and interglacial periods in Canada and Alaska.

Colias scudderii mayi Chermock & Chermock

Figure 1, Tables 1 & 2

Description. Male (n=50). Wings usually elongate. Forewing length 25–30 mm, mean = 28 mm. Dorsal ground color usually medium yellow, sometimes pale or dark yellow. Black border of forewing usually broad, rarely narrow, with yellow veins. Black discal spot of forewing usually large and prominent, round to oblong, sometimes reduced and faint. Black basal suffusion on fore and hindwings greatly reduced or completely absent. Discal spot on dorsal hindwing usually pale to medium orange, sometimes faint yellow. Black scaling in medial area of ventral forewing usually absent. Ventral ground color of hindwing yellow or orange. Black melanic scaling on ventral hindwing usually reduced or absent, but often heavier in Rocky Mountain populations. Discal spot on ventral hindwing ringed with red, variably large (37–38%), medium (28–32%), or small (31–34%). A satellite spot is usually present (66–89%), sometimes absent (11–34%).

Female (n=24). Forewing length 26–32 mm, mean = 29 mm. Dorsal ground color usually yellow, sometimes orange in western populations, white or cream in eastern populations. Black border of dorsal forewing variable, usually absent (41–57%) or partially present (29–41%), rarely fully developed (14–18%). Discal spot of dorsal hindwing pale to dark orange. Ground color of ventral hindwing yellow to orange. Other characters as in male.

Distribution and ecology. This subspecies is widely distributed across central Canada. It extends from southeast Manitoba west across central and northern portions of Manitoba, Saskatchewan, and Alberta to the Rocky Mountains, and southward along the eastern slope of the mountains to Glacier County, Montana. There is an isolated population in the Cypress Hills of Saskatchewan (Layberry *et al.* 1998). Northward, the distribution extends into the southern portions of the Northwest Territory around the Great Slave Lake. Westward, it extends throughout northeast British Columbia, and southward through the drainage of the Fraser River valley to about Jesmond, British Columbia (Guppy & Shepard 2001). In ecology, *C. s. mayi* occupies willow bogs in the taiga forest zone across central Canada, and in more isolated bogs further south in the mixed conifer-aspen parkland zone (Bird *et al.* 1995; Layberry *et al.* 1998).

Discussion. *Colias s. mayi* is the most divergent subspecies of *C. scudderii*, both from the Colorado *C. s. scudderii* and from West Coast forms of *C. occidentalis*, and is recognized by many distinctive characters. These include (1) very large size, (2) elongate wings, (3) deeper yellow dorsal ground color, (4) little or no black basal suffusion on dorsal wings, (5) often reduced or absent black melanic scaling on the ventral hindwing, (6) monomorphic yellow or orange ground color on the ventral hindwing, and (7) nearly monomorphic yellow females.

Ferris (1987) failed to recognize the distinctive

differences between this subspecies and the northern sub-arctic *C. s. gigantea*, apparently because of the clinal intergradation between the two subspecies in northern Manitoba. However, Masters (1970) correctly identified the above distinctions, and recognized *C. s. mayi* as an important evolutionary segregate. There is some minor geographic variation across Canada. Populations in the Rocky Mountains tend to show more black melanic scaling on the ventral hindwing compared to more eastern populations, and are nearly monomorphic for yellow females. Orange females are somewhat frequent in Rocky Mountain populations (12%), and may represent a residue from past hybridization with orange forms of *C. occidentalis*. These are usually mis-identified as females of *C. o. christina*.

As discussed by Masters (1970) and Ferris (1987), there is an apparent zone of clinal intergradation with *C. s. gigantea* in Manitoba, resulting in a higher frequency of white or cream females in eastern populations. Nevertheless, the hybrid suture zone between the two subspecies appears to be rather abrupt across much of Canada, similar to the abrupt suture zones of *Limenitis arthemis/astyanax* (Nymphalidae) and *Papilio glaucus/canadensis* (Papilionidae).

We suggest that *C. s. mayi* evolved as a northeastern segregate from *C. s. kohleri* in the taiga zone of central Canada centered in Manitoba during the Pleistocene. Its distribution has probably expanded and contracted periodically with the climatic fluctuations of the Pleistocene, following the north and south movements of the taiga zone on the northern Great Plains. During periods of glacial maxima, the distribution probably spread southward on the plains of eastern Montana and North Dakota, and moved north again back into Canada during warm interglacial periods. We suspect that *C. s. mayi* spread westward to the northern Rocky Mountains of Alberta and into British Columbia more recently since the retreat of the last glacial maxima about 12,000 years ago.

Colias scudderii gigantea Strecker

Figure 1, Tables 1 & 2

Description. Male (n=32). Forewing length 24–28 mm, mean = 26 mm. Dorsal ground color pale yellow. Black border of forewing usually broad, rarely narrow, with yellow veins. Black discal spot of forewing variable, round to oblong, sometimes large and prominent, often reduced and faint. Black basal suffusion on fore and hindwings usually moderate, sometimes light to heavy. Discal spot on dorsal hindwing pale yellow to orange. Black scaling in medial area of ventral forewing light to heavy, sometimes absent. Ventral ground color of hindwing usually yellow or orange, rarely green. Black melanic scaling on ventral hindwing moderate to heavy. Discal spot on ventral hindwing ringed with red, variably large (25–35%), medium (33–45%), or small (20–42%). A satellite spot is usually present (80–92%), sometimes absent (8–20%).

Female (n=16). Forewing length 25–29 mm, mean = 27 mm. Dorsal ground color usually white (67–70%) or cream (30–33%). Black border of dorsal forewing variable, often absent or partially present, sometimes fully developed. Discal spot of dorsal hindwing pale cream to orange. Ground color of ventral hindwing yellow, orange, or blue-green, often with very heavy black melanic scaling. Other characters as in male.

Distribution and ecology. As we narrowly define this subspecies, it is limited to true arctic or sub-arctic regions of Canada and Alaska. It is widely distributed throughout much of Yukon and Alaska extending to the south slopes of the Brooks Range, the Richardson Mountains, and west to the Seward Peninsula. Eastward, it extends to the Arctic Ocean in the Mackenzie River valley, the Great Bear Lake, and probably in the tundra-taiga ecotone regions of Northwest Territory to Hudson Bay. It then occurs to the southeast along the shores of Hudson Bay in Manitoba to the west shore of James Bay in Ontario.

C. s. gigantea occupies willow bogs in low arctic tundra and semi-forest taiga. Females have been observed ovipositing on *Salix reticulata* L. at Churchill, Manitoba (Ferris 1987). This subspecies appears to be particularly adapted to open tundra habitats, compared to the more taiga zone willow bogs of *C. s. mayi*. However, in central Alaska near Fairbanks and across central Yukon, it does occupy a more taiga semi-forest habitat.

Discussion. In sharp contrast to *C. s. mayi*, *C. s. gigantea* has experienced very little morphological divergence from *C. s. kohleri* and central Oregon forms of *C. occidentalis*. In fact, the only real difference among these taxa is the monomorphic white or cream forms of the female in *C. s. gigantea*. There is some range of variation in this subspecies. We have not seen what we would regard as a true yellow female form, but the cream form is frequently dark enough to approach yellow. Also, some females show a tinge or flush of orange on a white or cream background. Butterflies from low elevations in central Alaska near Fairbanks are often much larger in size like *C. s. mayi*, with a male forewing length of 27–29 mm. However, these still show the characters of typical *C. s. gigantea*.

A major problem with this subspecies is that there has long been confusion with arctic populations of sympatric *C. pelidne*. The latter is more narrowly limited to higher elevation montane habitats in the Mackenzie, Ogilvie, Richardson, and Brooks ranges of northwest Canada and Alaska. There appears to be considerable overlap in characters between the two species, possibly because of past hybrid introgression. We believe that Ferris (1987) actually illustrated the male and female of *C. pelidne* from the Ogilvie Mountains (his Figures 39–42), while his Figures 43–44

illustrate a typical male of *C. s. gigantea* from the Seward Peninsula. In general, males of the latter species closely resemble central Oregon forms of *C. occidentalis*, often with a strongly developed black discal spot on the dorsal forewing and a broad wing shape. By contrast, males of *C. pelidne* always have a very small, faint black discal spot with rather short, stubby wings. However, the most consistent difference between the two species may be size. Males of *C. pelidne* are consistently smaller with a forewing length of 22–24 mm (mean = 23 mm), while sympatric males of *C. s. gigantea* usually have a forewing length of 24–26 mm (mean = 25 mm).

We suggest that *C. s. gigantea* evolved as a far northern segregate from *C. s. kohleri* in the tundra-taiga zone of Alaska and Yukon during the Pleistocene. As with *C. s. mayi*, its distribution probably expanded and contracted periodically with the climatic fluctuations of the Pleistocene. During the last glacial maxima about 18,000 years ago, its distribution was probably confined to non-glaciated refugia in Yukon and Alaska (see discussion in Layberry *et al.* 1998). As the glacial ice sheets began to retreat across northern Canada about 10,000 years ago, *C. s. gigantea* spread eastward across Northwest Territory following the tundra habitat. It probably reached Hudson Bay during the warm hypsithermal period about 6000 to 9000 years ago (Layberry *et al.* 1998). At the same time, *C. s. mayi* was probably spreading northward into Manitoba from its glacial refugium on the northern Great Plains. Thus, the modern clinal intergrade zone in Manitoba between the two subspecies appears to be of very recent origin, taking place during this hypsithermal period.

An interesting biogeographic issue concerns biotic dispersal across Beringia between North America and Eurasia as discussed by Lafontaine & Wood (1988) and Layberry *et al.* (1998). Wolfe & Leopold (1967) have discussed the history of biotic interchange between Eurasia and North America during the Tertiary. Land bridges between the continents existed over Beringia and a North Atlantic connection over Greenland and Iceland up to the middle Miocene period, and then over Beringia through the Pliocene period. Tropical and subtropical biotas were exchanged between the continents through the Oligocene and Eocene periods about 25–40 million years ago, and warm temperate biotas were continuous across the continents during the early to middle Miocene about 15–25 million years ago.

However, all land connections may have been broken by seaways during the late Miocene about 7–15 million years ago as climatic conditions became cooler at high latitudes. This allowed boreal or taiga type conifer forests to evolve independently in Eurasia and North

America (Wolfe & Leopold 1967). The Beringia connection between Alaska and Siberia was re-established in the Pliocene about 3–7 million years ago, allowing a new interchange of a cold-adapted tundra biota to spread across the northern portions of the continents. However, some authors such as Petrov (1967) believe this Beringian connection was mostly broken during the Pleistocene. During periods of glacial maxima, much of Beringia was covered with either glacial ice sheets or cold, xeric grasslands rather than shrub tundra, while the Bering Strait seaway separated Alaska and Siberia during warm interglacial periods of the Pleistocene (Hopkins 1967).

These considerations are directly relevant to the inter-change of Lepidoptera populations between Eurasia and North America such as species of *Colias*. The *Vaccinium*-feeding group of *Colias* has clearly dispersed back and forth between North America and Eurasia on at least three separate occasions. The ancestral *C. pelidne* is thought to have originally dispersed from Alaska into Siberia in the early Pliocene, producing the *C. palaeno* radiation across the entire boreal region of Eurasia. This species then dispersed back across Beringia into North America to produce the modern *C. chippewa*, and this latter species dispersed a third time from Alaska into Siberia to produce *C. c. gomojunovae* Korshunov. All of these dispersal events must have taken place in the Pliocene or early Pleistocene about 1–7 million years ago if Hopkins (1967 p. 472), Petrov (1967), and others are correct that the Beringian connection between the continents was mostly broken during the late Pleistocene with respect to shrub tundra.

In sharp contrast, *C. scudderii* is widely distributed throughout most of Alaska today, extending west to the Seward Peninsula. Yet it has never been able to disperse across Beringia into Siberia. Certainly the boreal willow bog-tundra habitat is widespread across the northern regions of Eurasia. This evidence suggests that Petrov (1967) may be correct. *Colias scudderii* probably evolved in North America during the middle Pleistocene, and reached Alaska too late to successfully disperse across Beringia into Eurasia. The *C. pelidne* adaptive radiation is much older, and had no problem in dispersing repeatedly between the continents during the Pliocene or early Pleistocene.

Colias scudderii inupiat Harry

Description (from Harry 2007). Male (n=43). Forewing length 20–25 mm, mean ~ 23 mm. Dorsal ground color pale yellow. Black border of forewing usually medium broad with yellow veins. Black discal spot of forewing usually reduced to absent. Black basal suffusion on fore and hindwings moderate to heavy. Discal spot on dorsal hindwing pale yellow to orange. Black scaling on ventral forewing light to moderate. Ventral hindwing ground color yellow-

orange, usually with strong green over-scaling. Black melanic scaling on ventral hindwing moderate to heavy. Discal spot on ventral hindwing ringed with red, sometimes with a satellite spot.

Female (n=17). Forewing length 23–27 mm, mean ~ 25 mm. Dorsal ground color usually yellow or cream. Black border of dorsal forewing variable, often absent or partially present, sometimes fully developed. Discal spot of dorsal hindwing orange. Other characters as in male.

Distribution and ecology. This subspecies was recently described from extreme northern Alaska north of the Brooks Range (Harry 2007). It occupies the foothills and coastal plain between the mountains and the Arctic Ocean. Although collection records are confined to the vicinity of the Dalton Highway, the subspecies is probably widely distributed across northern Alaska between the Brooks Range and Arctic Ocean.

Harry (2007) describes the habitat as low boggy tundra, and in bogs along small streams in the Sagwon Hills. Females were observed ovipositing on *Salix lanata* L.

Discussion. *Colias s. inupiat* differs from *C. s. gigantea* in very small size, more greenish over-scaling on the ventral hindwing, and monomorphic yellow or cream females. Both subspecies appear to be northern segregates derived from *C. s. kohleri*, which is polymorphic with yellow, cream, and white females.

Hopkins *et al.* (1982) illustrate the known extent of glaciation in Beringia during the last glacial maxima about 20,000–14,000 years ago. The combined Laurentide and Cordilleran ice sheets covered most of Canada extending through southern and eastern Yukon, and the St. Elias and Alaska Ranges were heavily glaciated across southern Alaska. The Brooks Range was also heavily glaciated across northern Alaska. However, most of western and central Alaska was non-glaciated, extending east through the Yukon River drainage of western Yukon. The arctic coastal plain north of the Brooks Range was also non-glaciated, as was the Beringian land bridge connection with Siberia. As discussed by Hopkins *et al.* (1982), most of this land is thought to have been covered with a very xeric arctic steppe or mammoth steppe composed of bunchgrasses and xeric herbs such as *Artemisia* spp. (Asteraceae). Such steppes supported herds of large mammals such as the woolly mammoth. The mesic birch-heath shrub tundra with dwarf willows is thought to have been very narrowly restricted at this time to the edge of montane glaciers where moisture from melting ice was available. This is why *C. scudderii* was probably unable to spread westward across the mammoth steppes of Beringia into Siberia during the Pleistocene.

Thus, we suggest that ancestral populations of *C. s. kohleri* with polymorphic females spread northward into Alaska from the Rocky Mountains during a warm

interglacial period, possibly during the Sangamon Interglaciation about 120,000 years ago (Hopkins *et al.* 1982). During later periods of glaciation, separate populations became isolated north and south of the Brooks Range. Populations in the Yukon River drainage of central Alaska and eastern Yukon evolved into the modern *C. s. gigantea* with monomorphic white or cream females, while populations on the arctic coastal plain north of the Brooks Range evolved into the modern *C. s. inupiat* with monomorphic yellow or cream females. Of course, we have no way to know the exact timing of these events, since at least four major glacial-interglacial cycles are known to have impacted Beringia over the past 400,000 years (Hopkins *et al.* 1982). It is quite possible that *C. s. inupiat* has been isolated on the arctic coastal plain for a very long time, surviving through a number of Pleistocene climatic cycles.

***Colias scudderii nortepacifica* Hammond & McCorkle, new subspecies**

Figure 1

Description. **Male** (n=2). Forewing length 25–26 mm. Dorsal ground color pale yellow. Black border of forewing broad with yellow veins. Black discal spot of forewing large and prominent, round to oblong. Back basal suffusion on fore and hindwings very heavy. Discal spot on dorsal hindwing pale yellow to orange. Black scaling in medial area of ventral forewing light to absent. Ventral ground color of hindwing yellow to pale yellow-orange. Black melanic scaling on ventral hindwing very heavy. Discal spot on ventral hindwing ringed with red, variably small to large. A satellite spot is variably present or absent.

Female (n=1). Forewing length 27 mm. Dorsal ground color yellow. Black border of dorsal forewing fully developed, with the inner border forming a thin black line and the outer border faint and dusky. Discal spot of dorsal hindwing orange. Ground color of ventral hindwing yellow-orange with very heavy black melanic scaling. Other characters as in male.

Holotype. male, British Columbia, Nimpo Lake, 28 July 1962, A.L. Alderman leg. The holotype is deposited in the Oregon State Arthropod Collection, Oregon State University, Corvallis, Oregon, USA. **Allotype.** female, same data and deposition as holotype.

Paratype. male, British Columbia, Tatla Lake near Hwy. 20, 23 July 1981, Jon and Sigrid Shepard legs., deposition as holotype.

Etymology. The name refers to the Pacific Northwest.

Distribution, diagnosis and discussion. We have identified a very unusual isolate of *C. scudderii* that appears to be narrowly endemic to a remote region of southwest British Columbia. At present, it is only known from the three type specimens. These were originally identified as *C. occidentalis* based upon the very heavy black basal suffusion on the dorsal wings, and the heavy black melanic scaling on the ventral hindwing. However, these specimens differ from the typical form of *C. occidentalis* that is nearly parapatric in the drainage of the lower Fraser River valley by having a pale yellow or yellow-orange ground color on the

ventral hindwing. The female has the black wing border of the *C. scudderii* type in which the inner border is present as a thin, black line, while the outer border is dusky and obscure. In sharp contrast, *C. occidentalis* has a dark orange ground color on the ventral hindwing, and the female wing border is usually more solid black at the outer border and more dusky and obscure at the inner border.

The parapatric *C. s. mayi* in the drainage around the middle Fraser River valley is also distinctly different from this new subspecies. It often has a dark orange ground color on the ventral hindwing, often with greatly reduced black melanic scaling. In addition, it differs sharply from both parapatric *C. occidentalis* and *C. s. nortepacifica* in having little or no black basal suffusion on the dorsal wings.

At present, this new subspecies is only known along Highway 20 from Tatla Lake northwest to Nimpo Lake just east of Tweedsmuir Provincial Park. As discussed by Guppy & Shepard (2001), most of British Columbia was covered with glaciers during the last glacial maxima about 18,000 years ago. However, there must have been a non-glaciated refugium in southwest British Columbia at this time, probably in the rain shadow of the Coast Mountains east of Tweedsmuir Provincial Park within the larger Chilcotin River region. A number of distinctive butterfly taxa are endemic to this region and to south-central British Columbia in general, including *C. alexandra columbiensis* Ferris (Pieridae), *Speyeria aphrodite columbia* Hy. Edwards, *S. callippe chilcotinensis* Guppy & Shepard, *S. mormonia jesmondensis* dos Passos & Grey, a form of *S. atlantis beani* Barnes & Benjamin (= *S. hesperis* of some authors), and a very dark melanic form of *S. zerene picta* McDunnough (all Nymphalidae).

We suggest that *C. s. nortepacifica* evolved as a fourth segregate from the Rocky Mountain *C. s. kohleri* in the upper Pacific Northwest during the Pleistocene. However, while both *C. s. mayi* and *C. s. gigantea* were able to achieve wide and successful distributions during the Pleistocene, *C. s. nortepacifica* was nearly exterminated by the widespread glaciations in British Columbia. Only a few populations appear to have survived into the modern day as relicts within a non-glaciated refugium. The subspecies may be quite sedentary with limited dispersal abilities. By contrast, *C. s. mayi* is thought to have entered British Columbia quite recently from Alberta, first moving west through the Peace River drainage, extending northwest-ward towards Yukon, and southward through the Fraser River drainage to about Jesmond around 10,000 years ago as the glaciers retreated from central British Columbia. There is no evidence at this time of any genetic contact

or intergradation between *C. s. mayi* and *C. s. nortepacifica*.

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NEARCTIC EUCOSMINI (TORTRICIDAE) ASSOCIATED WITH *PELOCHRISTA OCCIPITANA* (ZELLER) AND *EUCOSMA BIQUADRANA* (WALSINGHAM): TWO NEW SYNONYMIES AND FOUR NEW SPECIES

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ABSTRACT. *Pelochrista occipitana* (Zeller), a species misidentified in North American collections for more than eighty years, is reviewed, illustrated, and reassigned to *Eucosma* Hübner. Two new species, *Pelochrista ainsliei* and *Pelochrista kingi*, are described from material formerly determined as *occipitana*. *Eucosma mediotriata* (Walsingham), *Pelochrista reversana* (Kearfott), and *Pelochrista palpana* (Walsingham) are interpreted as close relatives of these new taxa, based on male genitalia, and *mediotriata* is transferred to *Pelochrista*. *Pelochrista gilligani*, a new species with affinities to *palpana*, is described from Utah. *Pelochrista fuscosparsa* (Walsingham) is also reviewed, and a previously unrecognized species from California with similarities to both *fuscosparsa* and *mediotriata* is described as *Pelochrista fuscotriata*. Finally, *Pelochrista palousana* (Kearfott) and *Pelochrista tahoensis* (Heinrich) are recognized as junior synonyms of *Eucosma biquadrana* (Walsingham), and an account of the superficially similar *Eucosma shastana* (Walsingham) is included for comparison. Illustrations are provided of the adults and genitalia of the above mentioned species, and distributional information is reported. Lectotypes are designated for the five species described by Walsingham.

Additional key words: *fuscosparsa*, *mediotriata*, *palousana*, *palpana*, *reversana*, *shastana*, *tahoensis*.

Paedisca occipitana Zeller was described in 1875 from a single male specimen collected by G. W. Belfrage in Texas. It was later transferred to *Eucosma* Hübner by Fernald [1903], and that is where it resided at the time of Heinrich's (1923) revision of Nearctic Eucosmini. The holotype, which had been retained by Zeller, passed by way of the Walsingham Collection to the Natural History Museum, London (BMNH), and Heinrich did not have an opportunity to examine it. As a result, he mistakenly identified as *occipitana* a specimen in the United States Museum of Natural History (USNM) that had been collected by C. N. Ainslie in New Mexico. In the eighty some years that have elapsed, Heinrich's illustration (1923, Fig. 226) of that male's genitalia has been the basis for many incorrect determinations of *occipitana*. The genital structure depicted in that photograph is now associated with *Pelochrista* Lederer, which no doubt explains the current placement (Powell 1983) of *occipitana* in that genus. The purposes of this paper are to illustrate the species to which the name *occipitana* properly applies and show that it belongs in *Eucosma*; to make available names for two new species of *Pelochrista* previously misinterpreted as *occipitana*; to review the current Nearctic members of *Pelochrista* that appear to be most closely related to these new taxa, based on male genitalia; and to describe two additional new species of *Pelochrista* that have affinities with members of this group.

The taxon illustrated by Heinrich (1923) as *occipitana* is described below as *Pelochrista ainsliei*, new species. It is one of six Nearctic species of Eucosmini in which the valva has, in addition to several spiniform setae at the

anal angle of the cucullus, a particularly large spine projecting from the ventral margin of the neck. A second such taxon, also misidentified in collections as *occipitana*, is described below as *Pelochrista kingi*, new species. The remaining members of the group are: *Eucosma mediotriata* (Walsingham), which is transferred here to *Pelochrista*, *Pelochrista reversana* (Kearfott), *Pelochrista palpana* (Walsingham), and a third new species described below as *Pelochrista gilligani*.

In assembling specimens for this study I encountered a previously unrecognized species from California that is superficially similar to some phenotypes of *mediotriata* but resembles *Pelochrista fuscosparsa* (Walsingham) in genitalic structure. It is described below as *Pelochrista fuscotriata*, new species, and an account of *fuscosparsa* is included.

Eucosma biquadrana (Walsingham) is another western taxon that has not been correctly identified in North American collections. Heinrich (1923) placed it close to *Eucosma palousana* (Kearfott) but was unable to compare male genitalia of the two species for lack of authoritatively determined specimens of *biquadrana*. In that same monograph, Heinrich described *Eucosma tahoensis*, based on three specimens that I judge to be *biquadrana*, and since then *biquadrana* material in North American collections has been referred consistently to *tahoensis*. I examined the types of *biquadrana*, *palousana*, and *tahoensis* and concluded that they represent a single taxon. Although the last two species are currently placed in *Pelochrista* (Powell 1983), I propose that *biquadrana* remain in *Eucosma* (until the distinction between the two genera can be

clarified) and that *palousana* and *tahoensis* be treated as junior synonyms. A brief account of *Eucosma shastana* (Walsingham), a little known species from California that is remarkably similar to *biquadrana* in forewing appearance, is included for comparison.

MATERIALS AND METHODS

The conclusions in this paper are based on an examination of 475 adult specimens and 116 associated genitalia preparations from the following institutional and private collections: American Museum of Natural History, New York (AMNH); Charles D. Bird, Erskine, Alberta (CDB); George J. Balogh, Portage, Michigan; Canadian National Collection, Ottawa, Ontario (CNC); Colorado State University, Fort Collins, Colorado (CSU); BMNH; Essig Museum of Entomology, UC Berkeley (EME); Todd M. Gilligan, Loveland, Colorado (TMG); Edward C. Knudson, Houston, Texas; Los Angeles County Museum of Natural History, Los Angeles (LACM); Greg R. Pohl, Edmonton, Alberta; Strickland Museum, University of Alberta, Edmonton (UASM); USNM, and Donald J. Wright (DJW). Forewing length (FWL), defined as distance from base to apex (including fringe), is presented as an indication of specimen size. It was measured to the nearest one tenth of a millimeter with a reticule mounted in a Leica MZ95 stereomicroscope. Aspect ratio (AR), calculated as FWL divided by medial forewing width, is used as a crude measure of forewing geometry and is reported as the average, rounded to two decimal places, of a few such calculations. The number of observations supporting a particular statistic is indicated by *n*. The line drawings were made with the aid of a Ken-A-Vision Microprojector (Model X1000-1). Adult images were edited in Adobe Photoshop CS. Some figures were flipped horizontally, so what appears in an illustration to be a right forewing or valva is in fact the left such item on the specimen. Morphological terminology follows Gilligan *et al.* (2008).

Genitalia were mounted on slides for examination under a compound microscope. When observed *in situ*, by brushing scales from the posterior end of the abdomen, the large ventral spine on the valval neck of male specimens in the *mediostriata* group projects medially and is oriented roughly perpendicular to the surface of the valva. However, on slide mounts it was intentionally flattened as much as possible into the plane of the valva to show the size and shape of both the spine and the bulge on the ventral margin of the neck that supports it. Nevertheless, in some of the illustrations the spines appear somewhat foreshortened, depending on the angle of inclination between the spine and the surface of the slide.

In the 1950's, Obraztsov examined the syntypes of *mediostriata*, *fuscosparsa*, *palpana*, *biquadrana*, and *shastana* and selected a lectotype for each species, but his designations were never published. For the sake of nomenclatorial stability, I've included those designations here. I examined the specimens and associated genitalia slides of *palpana*, *biquadrana*, and *shastana*. For *mediostriata* and *fuscosparsa*, I relied on 35 mm color slides of the adults and black and white photographs of the genitalia made by Obraztsov.

SPECIES ACCOUNTS

Eucosma occipitana (Zeller), **revised combination**
(Figs. 7, 8, 34, 37)

Paedisca occipitana Zeller 1875: 315.

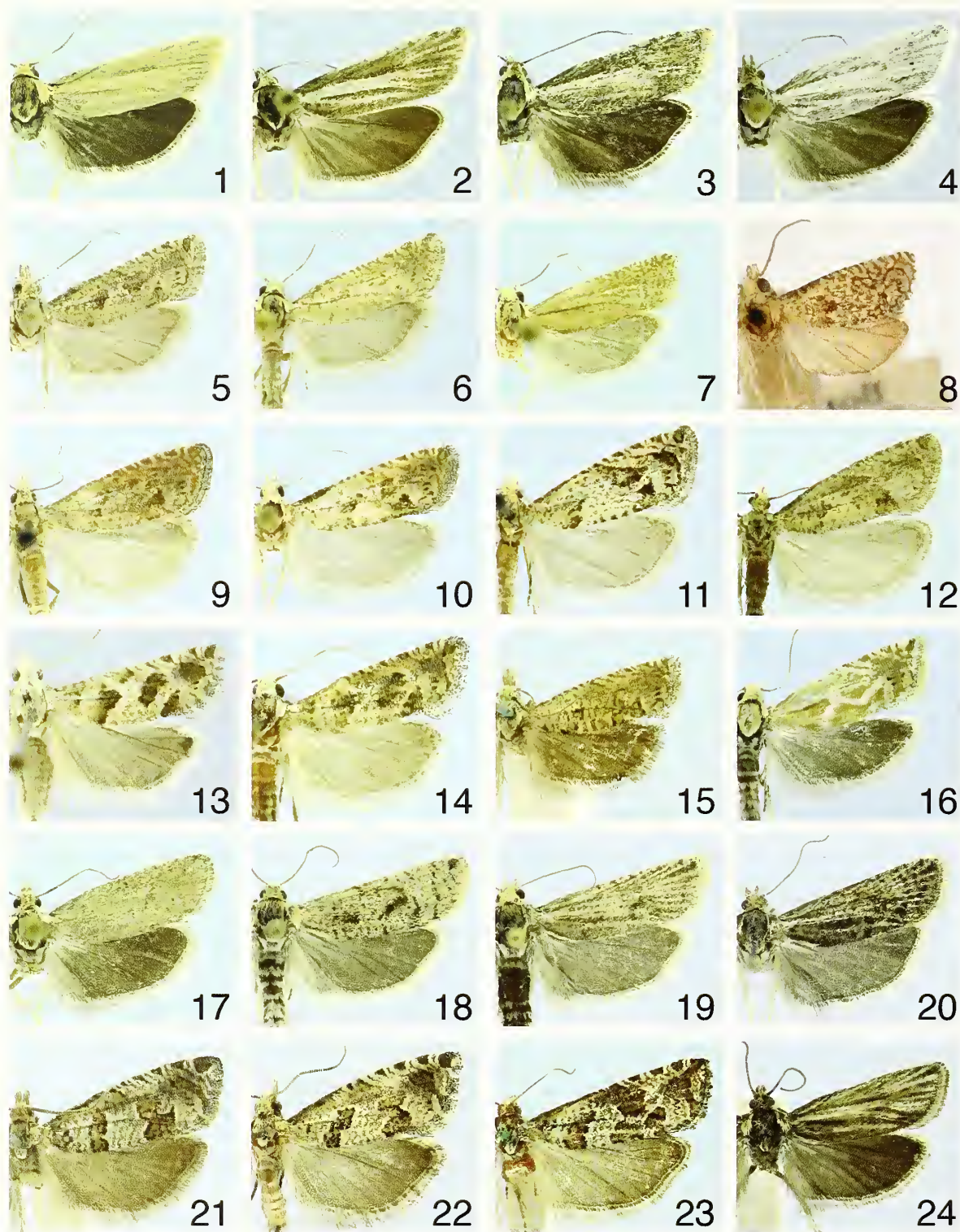
Eucosma occipitana: Fernald [1903]: 456; Barnes and McDunnough 1917: 169; Heinrich 1923: 111; McDunnough 1939: 47.

Pelochrista occipitana: Powell 1983: 35; Brown 2005: 480.

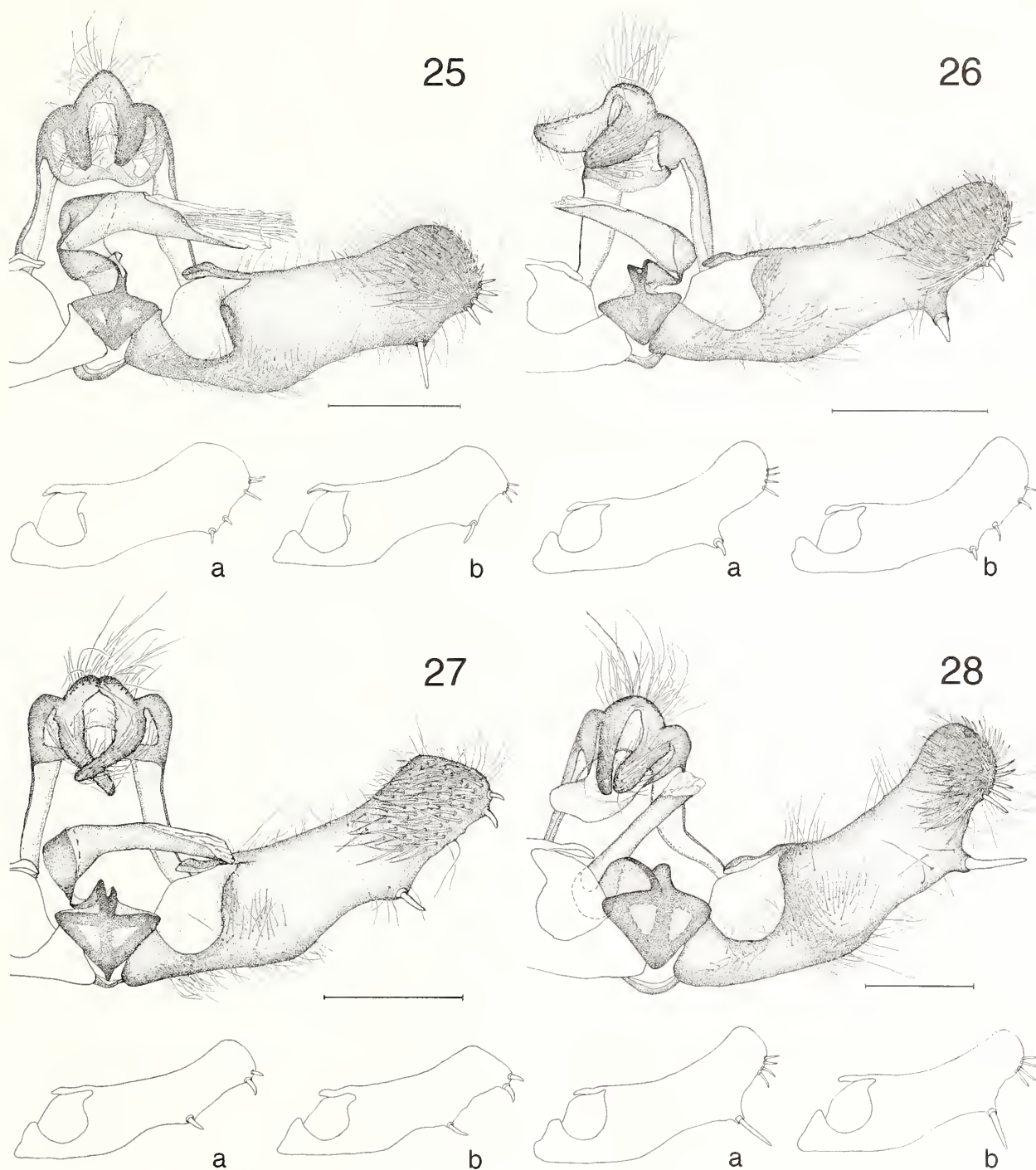
Discussion. The image of the holotype (Fig. 8) was provided by K. Tuck at the BMNH; that of its genitalia (Fig. 37) was obtained from a black and white negative made by Obraztsov of the slide he had prepared. Specimens other than the holotype that I located in institutional collections under the name *occipitana* all proved to be *P. ainsliei* or *P. kingi* (both described below). The specimen illustrated in Figure 7 is a male from Pawnee National Grassland, Weld Co., Colorado that I collected on 8 August 2004. Its forewing appearance is not an exact match to the holotype, but I have tentatively determined it as *occipitana* based on similarity of genitalia (Figs. 34, 37). The apparent differences in color could be a consequence of specimen age and/or photographic technique, and the more strongly mottled forewing appearance of the holotype might easily be attributed to variation. Of course, these issues cannot be resolved without additional material. In color, size, and forewing appearance, *occipitana* is similar to one of the phenotypes (Fig. 6) of *Pelochrista ainsliei* Wright and to *Eucosma kandana* Kearfott (Wright 2007, Fig. 12), but the three species are easily distinguished on the basis of male genitalia (Figs. 37, 26, & Wright 2007, Fig. 29). The shape and spining of the valva, together with the presence of a forewing costal fold, suggest that generic placement in *Eucosma* is appropriate.

Type. Holotype: ♂, Bosque Co., Texas, 24 June 1871, Bel-frage, genitalia slide 5756, BMNH.

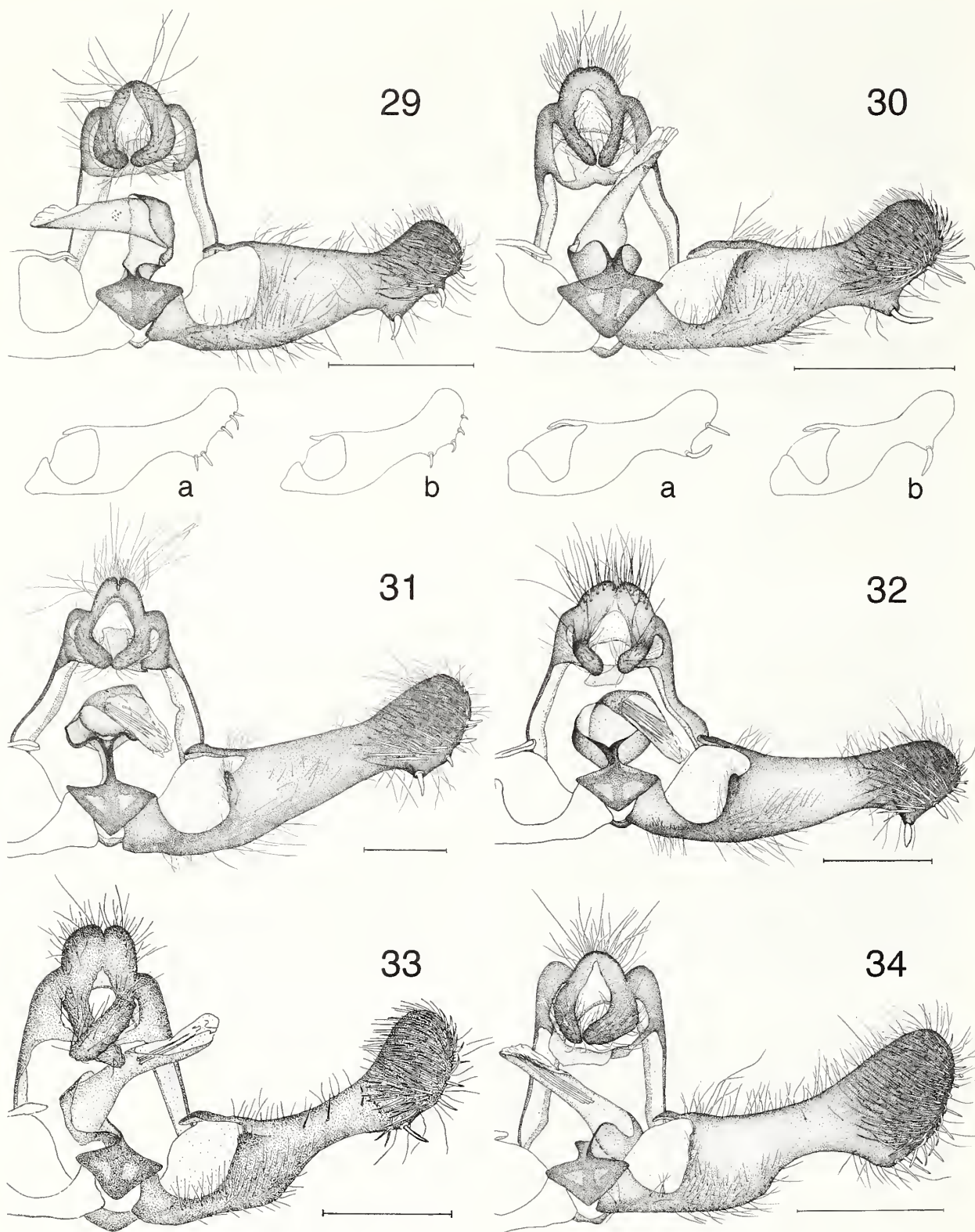
Descriptive notes. The dorsal surface of the forewing (Figs. 7, 8) is yellow brown to brown and somewhat mottled in appearance. There are no well defined fascial markings, and the ocellus is very weakly expressed. The specimen from Colorado has a FWL of 6.6 mm, with AR = 3.30.



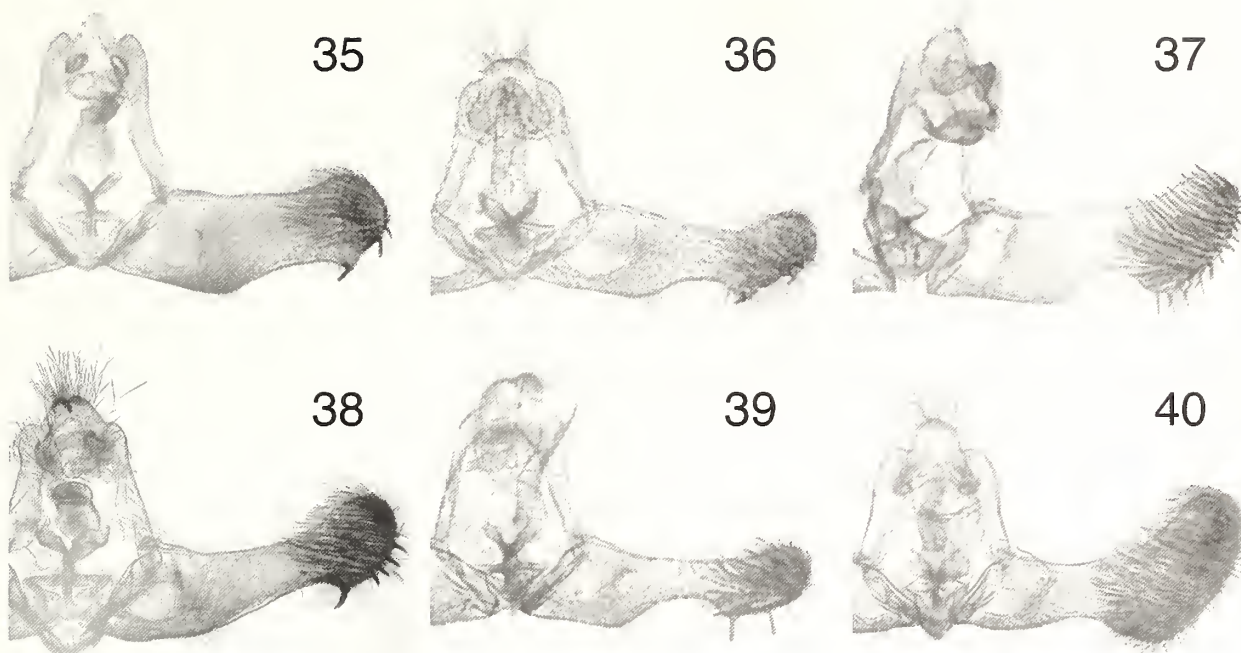
FIGS. 1-24. 1-4, *P. mediotriata*. 1, ♂ Albany Co., Wyoming. 2, ♂ Larimer Co., Colorado. 3, ♂ Sanpete Co., Utah. 4, ♂ Oneida Co., Idaho. 5-6, *P. ainsliei*. 5, ♂ Morgan Co., Colorado. 6, ♂ Otero Co., Colorado. 7-8, *E. occipitana*. 7, ♂ Weld Co., Colorado. 8, holotype, Texas. 9-11, *P. kingi*. 9, holotype, Saskatoon, Saskatchewan. 10, ♂ Albany Co., Wyoming. 11, ♂ Nordegg, Alberta. 12, *Pelochrista* sp., ♂ Sanpete Co., Utah. 13-14, *P. reversana*, ♂, ♂ Kimble Co., Texas. 15, *P. palpana*, lectotype, Shasta Co., California. 16, *P. gilligani*, holotype, Sanpete Co., Utah. 17-20, *P. fuscosparsa*. 17, ♂ Oneida Co., Idaho. 18, 19, 20, ♂, ♂, ♂ Albany Co., Wyoming. 21-22, *E. biquadrana*. 21, lectotype, Shasta Co., California. 22, ♂, Grant Co., Oregon. 23, *E. shastana*, lectotype, Siskiyou Co., California. 24, *P. fuscotriata*, holotype, San Mateo Co., California.



FIGS. 25–28. Male genitalia. **25**, *P. mediotriata*, slides DJW1863, 383, 966. **26**, *P. ainsliei*, slides DJW1859, 1344, 148. **27**, *P. kingi*, slides DJW1855, 1671, 1065. **28**, *P. reversana*, slides DJW1908, USNM70623, USNM70623. Scale bar = 0.5 mm.



FIGS. 29-34. Male genitalia. 29, *P. palpana*, slides DJW1924, USNM70633, DJW1158. 30, *P. gilligani*, slides DJW1911, 1912, 1912. 31, *P. fuscosparsa*, slide DJW1869. 32, *P. fuscostriata*, slide DJW1970. 33, *E. biquadrana*, (*palousana* lectotype), slide CH 20 April 1921. 34, *E. occipitana*, slide DJW 1138. Scale bar = 0.5 mm.



FIGS. 35–40. Male genitalia. **35**, *Paedisca mediotriata*, lectotype. **36**, *Paedisca palpana*, lectotype. **37**, *Paedisca occipitana*, holotype. **38**, *Paedisca fuscosparsa*, lectotype. **39**, *Paedisca biquadrana*, lectotype. **40**, *Paedisca shastana*, lectotype.

Male genitalia (Figs. 34, 37): Uneus a rounded, dorsally setose lobe; dorsolateral shoulders of tegumen well developed and humed; socii long, moderately setose and tapering distally; vesica with 6 (based on the one Colorado specimen) deciduous cornuti; valva with weakly concave costal margin, rounded apex, roughly right-angled anal angle, and moderately emarginated ventral margin; eueullus with 8–10 long spiniform setae evenly distributed along distal margin, the longest located near the anal angle; medial surface of eueullus densely covered with stout setae. **Female genitalia**: Unknown.

Pelochrista mediotriata (Walsingham), **new combination**
(Figs. 1–4, 25, 35, 41, 50)

Paedisca mediotriata Walsingham 1895: 508.

Eucosma mediotriata: Fernald [1903]: 460; Barnes and McDunnough 1917: 171; Heinrich 1923: 116, Fig. 245; McDunnough 1939: 47; Powell 1983: 34; Brown 2005: 323.

Eucosma sepulcrana Meyrick 1927: 334.

Eucosma sepulchrana: Clarke 1958: 420. [misspelling of *sepulcrana*].

Discussion. To make the comparison with *E. sepulcrana* Meyrick, Clarke (1958) dissected the specimen designated above as lectotype for *mediotriata*, but to my knowledge this choice of name bearing specimen for *mediotriata* has not been published previously.

The genitalia of the lectotype (Fig. 35) have a large spine on the ventral margin of the valval neck, which is

the reason for the proposed reassignment of this species to *Pelochrista*. Heinrich's illustration of *mediotriata* (1923, Fig. 245) shows no indication of the spine on either valva, but an examination of the associated slide revealed that both spines had been broken off at the socket and apparently lost.

Types. *Paedisca mediotriata*. Lectotype here designated: ♂, [Larimer Co.], Loveland, Colorado, 5000 ft., July 1891, Smith, genitalia slide JFGC6388, Wlsm. No. 31141, BMNH. Paralectotypes: Loveland, Colorado, July 1891; 1 ♂, 5–10,000 ft, Wlsm. No. 31119; 1 ♂, 10,000 ft., Wlsm. No. 31118; 1 ♂, 5000 ft., Wlsm. No. 31192; 1 ♂ [no elevation indicated], Wlsm. No. 30429; all in the BMNH. *Eucosma sepulcrana*. Lectotype designated by Clarke (1958): ♂, [Tooele Co.], Dividend, Utah, 26 June, genitalia slide JFGC6386, BMNH. Paralectotypes: 11 specimens [according to Meyrick (1927) and Clark (1958)], same data as lectotype, BMNH.

Descriptive notes. The specific name derives from the presence in most individuals of a prominent pale forewing streak running anterior to the cubitus from base to distal end of cell (Fig. 2). Often thin streaks of the same pale color are present along the costa, the median branches, CuA2, and A1+A2. The streaking is variable and, in some instances (Fig. 1), barely discernable. Forewing color is also variable, from yellowish brown (Fig. 1) to whitish gray (Fig. 4), with numerous intermediate combinations of yellow brown, olive brown, whitish gray, and blackish gray. There are no discernable fascial markings, and the ocellus is not expressed. The hindwing is black to blackish gray, with fringe varying from white to pale gray. Forewing statistics: ♂ FWL: 6.7–12.4 mm (mean = 10.1, n = 71), AR = 3.35; ♀ FWL: 8.1–11.8 (mean = 9.8, n = 14), AR = 3.21.

Male genitalia (Figs. 25, 35): Uneus semitriangular with rounded apex; socii fingerlike and moderately setose; vesica with 18–42 deciduous cornuti (n = 13); valva with raised clasperlike

process on margin of basal excavation and with large spine on ventral margin at distal end of neck; cucullus semirectangular, with 3 or 4 spiniform setae at anal angle. Figure 25 illustrates the variation in valval shape and in the spining of the ventral margin of the cucullus. *Female genitalia* (Fig. 41): Papillae anales laterally facing and sparsely setose; lamella antevaginalis ringlike; lamella postvaginalis well developed and semirectangular, with variably wrinkled lateral margins and a shallow medial trough from center of posterior margin to ostium; posterior margin of sternum 7 with weakly developed, convex, medial bulge; ductus bursae with small sclerotized patch at juncture with ductus seminalis; corpus bursae with one small signum.

Distribution and biology. Figure 50 shows the geographic distribution of *mediostriata*, based the 165 specimens (151 ♂; 14 ♀) in the study sample. Capture dates range from mid-April (in Texas) to early August, but the vast majority of the records are from June and July. No larval host has been reported.

Pelochrista ainsliei, new species

(Figs. 5, 6, 26, 43, 50)

Eucosma occipitana: (not Zeller 1875) Heinrich 1923: 111, Fig. 226; McDunnough 1939: 47.

Pelochrista occipitana: (not Zeller 1875) Powell 1983: 35; Brown 2005: 480.

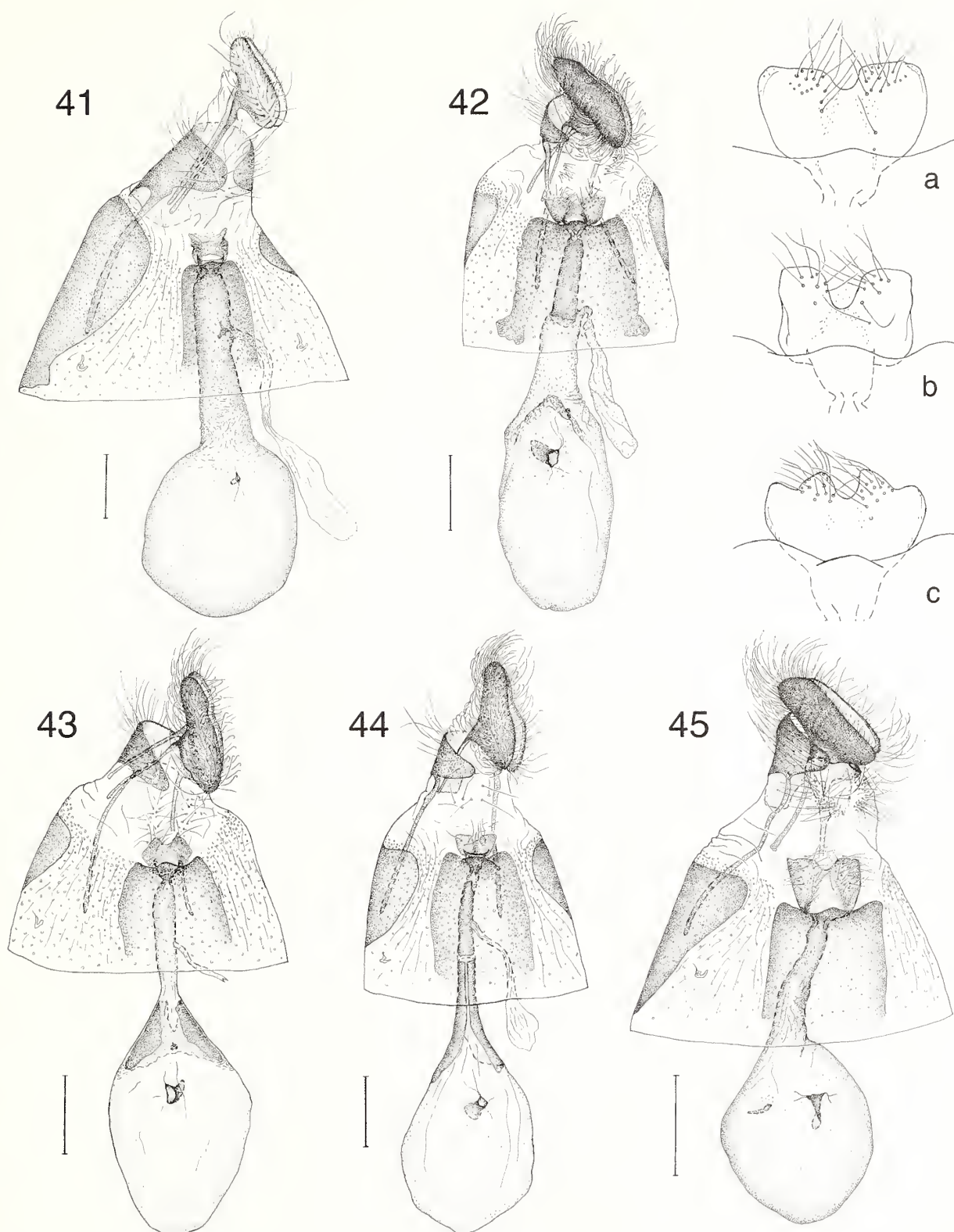
Diagnosis. This species is separated from other western *Eucosmini* of similar forewing pattern and coloration by features of the genitalia. Males are distinguished by the following combination of characters (Fig. 26): uncus moderately developed and not medially divided; ventral margin of valval neck not emarginated but with strongly developed projection supporting one particularly stout spine; and cucullus either rounded or with broadly rounded apex and anal angle, the latter with three or more spiniform setae. Distinctive female genitalic characters include (Fig. 43): diamond shaped lateral projections of lamella postvaginalis; medial projection of posterior margin of sternum 7 fused with sterigma; posterior one-fourth of corpus bursae sclerotized on dorsal and lateral surfaces; and corpus bursae with two signa. In size, color, and general appearance, the *ainsliei* phenotype with weakly expressed forewing markings (Fig. 6) is quite similar to *E. occipitana* (Fig. 7) and *E. kandana* Kearfott (Wright 2007, Fig. 12), but the three taxa have very different valvae (Figs. 26, 34 & Wright 2007, Fig. 29). Based on forewing pattern, well-marked specimens of *ainsliei* (Fig. 5) might be confused with *Pelochrista emaciatana* (Walsingham) (Wright 2005, Fig. 10). Moreover, females of these two species have rather similar sclerotized plates on the surface of the corpus bursae (Fig. 43, Wright 2005, Fig. 24). However, *emaciatana* is larger (mean FWL = 10.5 mm vs. 7.8 mm in *ainsliei*), it differs from *ainsliei* in the shapes of the cucullus and valval neck (Wright 2005, Fig. 17 vs. Fig. 26), and it has

only one signum in the corpus bursae. The apical area of the forewing in *ainsliei* lacks the reddish-brown suffusion that is prominent in many specimens of *kingi*. Genitalic differences between *ainsliei* and *kingi* are discussed below under the latter species.

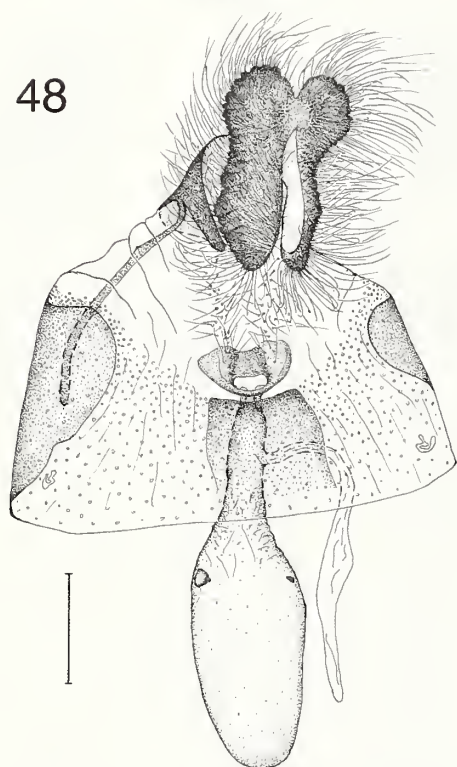
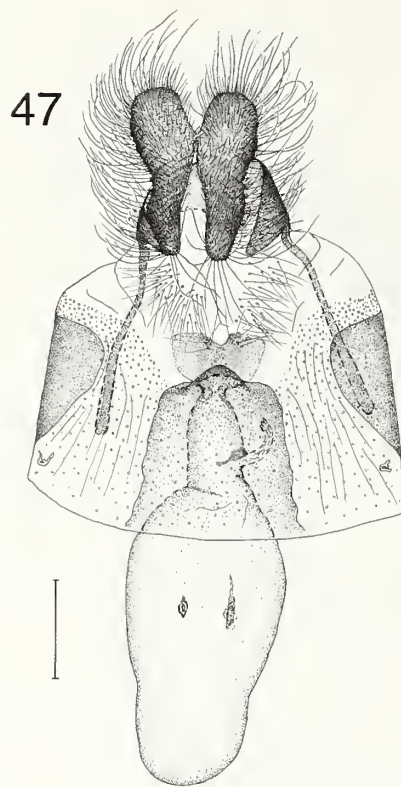
Description. *Head*: Frons white to pale tan, scales of vertex pale tan with white apices; labial palpi with medial surfaces white, lateral surfaces pale brown; antenna pale tan. *Thorax*: Dorsal surface concolorous with head; ventral surface whitish tan; legs pale brown, with whitish-tan tarsal annulations. *Forewing* (Figs. 5, 6): ♂ FWL 6.4–8.4 mm (mean = 7.7, n = 17), AR = 3.38; ♀ FWL 7.7–8.5 mm (mean = 8.1, n = 4), AR = 3.26; costa straight, apex acute, termen weakly convex; dorsal surface brown to yellowish brown, with variably expressed darker brown markings as follows: subbasal fascia an outwardly oblique bar from dorsum to radius, usually interrupted on A1+A2, median fascia consisting of a narrow dash at mid costa and an irregularly shaped blotch at distal end of cell, pretoral patch triangular and projecting anteriorly from dorsum along basal margin of ocellus; ocellus with pale tan central field, crossed longitudinally by up to three dark dashes, bordered basally and distally by transverse bars of lustrous pale-tan and/or silvery-white scales; a longitudinal patch of white-tipped brown scales anterior to ocellus extends basally nearly to the subbasal fascia, dividing the median fascia on the radius. *Hindwing*: Gray brown with paler fringe. *Male genitalia* (Fig. 26): Uncus a semitriangular, dorsally setose lobe; socius moderately setose, broad at base, tapering to narrowly rounded apex; gnathos bandlike; aedeagus long, tapering distally; vesica without cornuti; valva with costal margin weakly concave, cucullus weakly differentiated, and ventral margin of neck with strongly developed projection supporting a large spine-like seta; cucullus with apex and anal angle rounded, the latter with three or four spiniform setae; medial surface of cucullus covered with stout setae. *Female genitalia* (Fig. 43): papillae anales laterally facing, with long ventrally curving setae along lateral margins and hook-tipped setae along medial margins; lamella postvaginalis with diamond-shaped lateral extensions and a shallow, microspinulate, medial trough from V-shaped indentation of posterior margin to ostium; posterior extremities of sterigma and membrane between sterigma and ventral extremities of tergum 8 with numerous, long, hairlike setae; posterior margin of sternum 7 with medial triangular projection that fuses with lamella antevaginalis and shields ostium bursae; corpus bursae with large sclerotized plate at junction with ductus bursae, extending over dorsal and lateral surfaces but not closing ventrally; one small signum located at center of anterior margin of sclerotized patch, a second large signum on ventral surface of bursa.

Holotype. ♂, New Mexico, [Dona Ana Co.], Mesilla, C. N. Ainslie, genitalia slide USNM 70620, USNM.

Paratypes. COLORADO: Larimer Co., Fort Collins, 15 June 1920 (1 ♂), AMNH, 16 June 1920 (1 ♂), CSU; no locality data (1 ♂, genitalia slide USNM 70621), USNM; [Arapahoe Co.], Platte Can[y]on, Osler (1 ♂, genitalia slide USNM 70622), USNM; Morgan Co., 3.5 mi. W. of Co. Rd. 19 on Co. Rd. 1, 4610 ft. D. J. Wright, 28 July 1995 (1 ♂, genitalia slide DJW 148), DJW; Otero Co., Vogel Cyn. Picnic Area, 15 mi. S. of La Junta, 4340 ft. D. J. Wright, 18 August 1997 (1 ♂), DJW; Otero Co., Comanche NG [National Grassland], 15 mi. S. of La Junta, D. J. Wright, 27 August 2000 (2 ♂), DJW; Weld Co., Pawnee Site, L.T.E.R. USDA, P. A. Opler, 27 July 1991 (2 ♂), CSU; 0.25 mi. N. 1–76 on CR 91, T. M. Gilligan & P. A. Opler, 17 August 2007 (1 ♀, genitalia slide DJW 1909), TMG; Pawnee NG, Jct CR-96 & CR-61, 5030 ft., T. M. Gilligan & P. A. Opler, 31 August 2007 (1 ♂, genitalia slide DJW 2039; 1 ♀, genitalia slide DJW 2038), TMG. NEW MEXICO: Same data as holotype (2 ♂, 2 ♀; genitalia slides DJW 1860, 1984, USNM; 1 ♂, genitalia slide DJW 1344, AMNH; 1 ♂, LACM). WYOMING: [Weston Co.], 6 mi. NW Newcastle, R. W. Hodges, 23 June 1965 (1 ♂, genitalia slide DJW 1859), USNM.



FIGS. 41–45. Female genitalia. 41, *P. mediotriata*, slide DJW1862. 42, *P. reversana*, slides USNM95247, DJW1926, USNM90506, DJW1925. 43, *P. ainsliei*, slide DJW1860. 44, *P. kingi*, slide DJW1856. 45, *P. palpana*, DJW 771. Scale bar = 0.5 mm.



FIGS. 46–49. Female genitalia. 46, *P. fuscosparsa*, slide DJW1871. 47, *P. fuscostriata*, slide DJW1971. 48, *E. biquadrana*, slide DJW1596. 49, *E. shastana*, slide DJW1973. Scale bar = 0.5 mm.

Etymology. This species is named in honor of Charles N. Ainslie, a cercal entomologist who worked for the Federal Bureau of Entomology from 1906 to 1930 (Walton & Caffrey 1940). His specimens of *ainsliei* from Mesilla, New Mexico seem to be the first collected examples. Though the pin labels do not indicate date of capture, it is likely these specimens were collected in 1908, when Ainslie was on assignment to New Mexico to study a population peak of *Hemileuca oliviae* Cockerell (Saturniidae).

Distribution and biology. The type series consists of 21 adults (17 ♂, 4 ♀) from Colorado, New Mexico and Wyoming (Fig. 50). Capture dates, which are available for only 13 of the specimens, range from 15 June to 31 August. No larval host is known.

Remarks. The holotype of *ainsliei* is the specimen illustrated by Heinrich (1923, Fig. 226) as *occipitana*. The shape of the cucullus is variable, as indicated in Fig. 26. All specimens have the large spine on the ventral margin of the neck and a cluster of three or four smaller spines near the anal angle of the cucullus, but in some individuals (Fig. 26b) one spine seems to be displaced to midway between these positions. In a given specimen, this condition may be present on one valva and absent on the other.

Pelochrista kingi, new species

(Figs. 9–11, 27, 44, 50)

Diagnosis. This species often can be distinguished from congeners with similar forewing markings by the presence of at least some reddish-brown suffusion in the apical portion of the forewing. The male genitalia (Fig. 27) are similar to those of *ainsliei* (Fig. 26), but the uncus is distinctly divided medially, the socii are narrower, the support for the large spine on the ventral margin of the neck is less strongly developed, the cucullus is semirectangular, and the anal angle of the cucullus usually has only two spiniform setae. Females (Fig. 44) are characterized by the ringlike lamella antevaginalis, the nearly complete sclerotization of the ductus bursae, and the presence of only one signum in the corpus bursae.

Description. *Head:* Frons and vertex white to pale tan, vertex scales sometimes marked medially with pale grayish brown; labial palpi with medial surfaces white, lateral surfaces pale grayish brown; antenna concolorous with vertex. *Thorax:* Dorsal surface concolorous with head but often a shade darker, ventral surface pale whitish tan; legs brown with whitish tarsal annulations. *Forewing* (Figs. 9–11): ♂ FWL 7.9–10.0 mm (mean = 8.9, n = 25), AR = 3.14; ♀ FWL 8.0–8.9 mm (mean = 8.4, n = 7), AR = 3.04; costa and termen weakly convex, apex acute; dorsal surface tan to grayish brown with brown to blackish-brown markings; termen and distal one half of costa with reddish-brown suffusion; subbasal and median fasciae variably expressed, the former an outwardly oblique bar from dorsum to radius that is often interrupted on A1+A2, the latter an irregularly shaped mark at dis-

tal end of cell that is connected to the costa by a barely discernable brownish streak; pretornal patch irregular in shape and extending anteriorly from dorsum along basal margin of ocellus; costal fold darker than adjacent interfascial scaling; ocellus with brownish central field crossed longitudinally by up to four dark dashes and bordered basally and distally by lustrous gray transverse bars; apex and termen lined with about five rows of scales with bright white apices and sharply contrasting, dark, grayish-brown, medial markings. *Hindwing:* Pale grayish brown. *Male genitalia* (Fig. 27): Uncus weakly developed and divided medially; dorsolateral shoulders of tegumen hunched; socii long, narrowing distally, and moderately setose; gnathos bandlike; aedeagus long and narrow; vesica without cornuti; valva with costal and ventral margins nearly parallel and with a weakly developed projection on ventral margin at mid neck supporting a large spiniform seta; cucullus semirectangular; apex obtuse to right-angled; anal angle often narrowly rounded but with moderately developed ventral projection in some individuals (Fig. 27b), in either case supporting two large spiniform setae; medial surface of cucullus covered with stout setae. *Female genitalia* (Fig. 44): Papillae anales laterally facing, lateral margins with long ventrally curving setae, medial margins sinuate and lined with hook-tipped setae; sterigma ringlike anteriorly; lamella postvaginalis a shieldlike plate with a shallow central trough joining ostium to medial indentation in posterior margin; posterior margin of sternum 7 bulging ventrally and weakly shielding ostium; sclerotization of sternum 7 more strongly pronounced along posterior and lateral margins, ductus bursae almost entirely sclerotized, but with a narrow membranous ring between juncture with ductus seminalis and corpus bursae and with a narrow membranous strip on ventral surface from ring to corpus bursae, anterior component of sclerotization projecting laterally on surface of corpus bursae; corpus bursae with one large signum on ventral surface.

Holotype. ♂, CANADA, Saskatoon, Saskatchewan, 26 July 1923, Kenneth M. King, CNC.

Paratypes. CANADA: ALBERTA: Dry Island Prov. Pk., C. D. Bird, 15 August 2004 (1 ♂, genitalia slide DJW 1458), CDB; Jasper, J. McDunnough, 24 July 1926 (1 ♂, 5 ♀, genitalia slides DJW 1856, 1858), CNC; Lethbridge, H. L. Seamans, 4 July 1922 (1 ♂, genitalia slide TOR 3258), 16 July 1922 (1 ♂), CNC; Nordegg, J. McDunnough, 24 July 1921 (1 ♂, genitalia slide TOR 3257), 25 July 1921 (1 ♂, genitalia slide DJW 1857), CNC; K. Bowman, 24 July 1922 (1 ♂), 22 July 1933 (10 ♂), UASM. BRITISH COLUMBIA: 100 Mile [Mile ?] House, C. S. Walley, 4 July 1938 (1 ♀), CNC; Jesmond, J. K. Jacob, 5000', 15 July 1937 (1 ♂), 23 July 1938 (1 ♀), CNC; Kamloops, J. K. Jacob, 20 June 1937 (1 ♂, genitalia slide TOR 3260), CNC. SASKATCHEWAN: Indian Head, J. J. de Gryse, 22 July 1925 (1 ♂), 26 July 1925 (1 ♂, genitalia slide TOR 3259), CNC. USA: ARIZONA: [Coconino Co.], North Rim, Crickmer, August 1949 (1 ♂, genitalia slide DJW 1983) USNM. MONTANA: Carter Co., Medicine Rocks SP, George J. Balogh, 5 September 2002 (1 ♂, genitalia slide DJW 1095), DJW. SOUTH DAKOTA: [Yankton Co.], Yankton, M. O. Clemm, 3 August 1949 (1 ♂, genitalia slide DJW 1065), USNM. WYOMING: Albany Co., 2217 Sky View Lane, 7468', J. S. Nordin, 23 June 2007 (1 ♂, genitalia slide DJW 1855), 1 August 2006 (1 ♂, genitalia slide DJW 1671), DJW.

Etymology. The specific epithet honors Kenneth M. King, a Dominion Entomologist based at the Agriculture Canada station at Saskatoon, Saskatchewan during the 1920's and 1930's.

Distribution and biology. The type series consists of 33 adults (26 ♂, 7 ♀) from Alberta, British Columbia, Saskatchewan, Arizona, Montana, South Dakota, and Wyoming (Fig. 50). Capture dates range from 20 June

to 5 September, but most specimens were collected in July. No larval host is known.

Remarks. The collection sites in the Canadian Provinces, Montana, and South Dakota are at elevations ranging from roughly 1200 ft to 5000 ft.; those in southeastern Wyoming and Arizona are at about 7500 ft and 8290 ft., respectively. I examined 13 specimens in the AMNH collected by F. Rindge that I am tentatively determining as *P. kingi* due to general agreement in forewing appearance and male genitalia. Ten were taken on 25–30 July 1967 at 8800 ft. along St. Louis Creek, Grand Co., Colorado; the other three on 10–11 August 1959 at ca. 10,000 ft in Carbon Co., Wyoming. I did not include this material in the type series because the apical area of the forewing has only a faint indication of reddish-brown suffusion, and no females were available for comparison. I have seen similar but grayer specimens (Fig. 12) collected at 10,100 ft. along Ephraim Canyon Road, Sanpete Co., Utah. This last material may represent another new species, but the male genitalia are not sufficiently distinctive to support that conclusion, and I have seen no associated females. These subtle differences in forewing coloration might be the result of altitude adaptation in a single species.

Pelochrista reversana (Kearfott)

(Figs. 13, 14, 28, 42, 50)

Eucosma reversana Kearfott 1907: 22; Barnes & McDunnough 1917: 170; Heinrich 1923: 112, Fig. 223; McDunnough 1939: 47.

Pelochrista reversana Powell 1987: 35; Brown 2005: 481.

Discussion. The description of *reversana* was based on three specimens belonging to Dr. William Barnes, all of which were collected at San Antonio, Texas. It appears that Kearfott kept two of the syntypes, a male and a female now residing in the AMNH, and the third, a male, was acquired by the USNM along with the Barnes collection. Heinrich (1923, Fig. 223) illustrated the genitalia of the male in the AMNH and labeled the slide TYPE, thus clearly selecting that specimen as the name bearer. He also pointed out that the female syntype is not *reversana* but rather *Eucosma exclusoriana* Heinrich, a somewhat smaller species which, based on male genitalia (Heinrich 1923, Fig. 160), is not a close relative of any of the species treated here.

Types. Lectotype designated by Heinrich (1923): ♂, [Bexar Co.], San Antonio, Texas, genitalia slide CH 16 Dec 1919, AMNH. Paralectotype: ♂, San Antonio, Texas, USNM.

Descriptive Notes. The forewing pattern of *reversana* (Figs. 13, 14) features conspicuous brown markings with whitish interfascial areas, the latter with pale orange-brown striations. The basal, subbasal and median fasciae are strongly expressed. The

subbasal fascia often is interrupted in the cell and on A1+A2 by bands of orange-brown to whitish-tan scales. The median fascia is represented by an outwardly oblique bar at the distal end of the cell and a dark rectangular mark at mid-costa, the two being at least weakly connected along the radius. A triangular pretorinal patch on the dorsum is separated from the median fascia by a band of whitish scales. The ocellus has a pale tan central field that is crossed longitudinally by three or four, short, dark dashes and is bordered basally and distally by transverse bars of lustrous white scales. Anterior to the ocellus is a large patch of scales with white to pale gray apices and dark grayish-brown medial markings. Forewing statistics: ♂ FWL: 7.7–10.7 mm (mean = 9.0, n = 17), AR = 3.20; ♀ FWL: 7.7–10.9 (mean = 9.1, n = 13), AR = 3.04. **Abdomen:** Intersegmental abdominal membrane between sternites 6 and 7 of female with a pair of pocketlike invaginations (not illustrated). **Male genitalia** (Fig. 28): Uncus a rounded, dorsally setose lobe; socii long, nearly uniform in width, and moderately setose; aedeagus long and narrow; vesica without cornuti; valva with a strongly developed projection on ventral margin of neck supporting a particularly large spine; cucullus narrower than neck, with apex rounded and with anal angle rounded and somewhat bulging; distal margin of cucullus densely lined with stout setae, the largest 3–4 located near anal angle; medial surface of cucullus covered with stout setae. **Female genitalia** (Fig. 42): Papillae anales laterally facing, with long ventrally curving setae on lateral margins and hook-tipped setae along margins of anal opening; lamella postvaginalis with variably shaped lateral extensions (Fig. 42), with a pronounced medial indentation in posterior margin, and with patches of long hairlike setae flanking the indentation; posterior margin of sternum 7 with weakly developed medial projection that fuses with the sterigma and partially shields the ostium; ductus bursae sclerotized from constriction anterior to ostium to juncture with ductus seminalis; juncture of corpus bursae and ductus bursae contorted by variable thickening and wrinkling of membrane; corpus bursae with a large signum on ventral surface and a small signum on thickened membrane of dorsal surface.

Distribution and biology. I examined 73 adults (54 ♂, 19 ♀) from Arizona, Colorado, Kansas, New Mexico, and Texas (Fig. 50). Three specimens were collected in mid-April; the rest between mid-July and mid-October. Most records are from August or September. The capture dates suggest the possibility of two generations per year in Texas. No larval host has been reported.

Pelochrista palpana (Walsingham)

(Figs. 15, 29, 36, 45, 51)

Paedisca palpana Walsingham 1879: 54.

Eucosma palpana: Fernald [1903]: 457; Barnes and McDunnough 1917: 170; Heinrich 1923: 113, Fig. 225; McDunnough 1939: 47.

Pelochrista palpana: Powell 1983: 35; Brown 2005: 480.

Discussion. In his description of *palpana*, Walsingham (1879) mentioned six syntypes (5 ♂, 1 ♀). One male is unaccounted for; the other five specimens are clearly labeled as indicated above and reside in the BMNH. In addition to the syntypes, there are 42 specimens that appear to have been collected by Walsingham, probably at the type locality. They are located as follows: 36 in the BMNH (K. Tuck, pers.

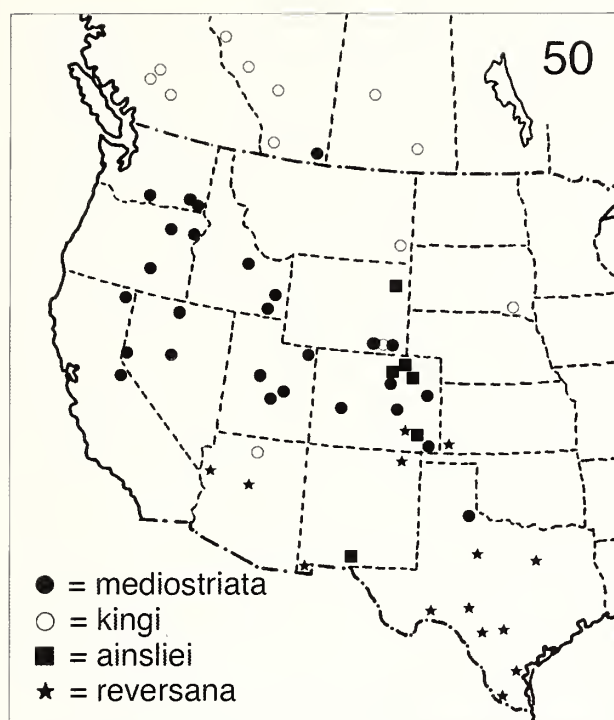


FIG. 50. Geographic distribution of *P. mediotriata*, *P. kingi*, *P. ainsliei*, and *P. reversana*.

comm.); 1 in the AMNH; and 5 in the USNM. The last five were part of the Fernald collection and bear the red-bordered determination labels typical of exemplars that Walsingham gave to Fernald. There is no capture data associated with them except for a reference to California, and three of the specimens were actually determined as *Paedisca graminana* Walsingham, a name that has never been published. The specimen in the AMNH has pin labels with the inscriptions "Cotype" and "Lord Walsingham Collection."

Types. Lectotype here designated (Figs. 15, 36): ♂, Pit River, Shasta Co., California, 21–26 July 1871, Walsingham, genitalia slide 11519, BMNH. Paralectotypes: same locality data as lectotype (3 ♂, 1 ♀, ♀ genitalia slide 11536, BMNH). [Walsingham (1879) mistakenly reported these specimens as collected in August.]

Descriptive Notes. The forewing is yellowish brown, with rather poorly defined darker brown markings (Fig. 15). The sub-basal fascia is usually discernable from dorsum to discal cell, its distal margin being marked with blackish-brown scales. There is an irregularly shaped pretornal patch on the dorsum abutting the proximal margin of the ocellus and a narrow post median band extending from costa to mid-termen. Often these markings contrast weakly with the interfascial coloration, resulting in a rather uniformly irrorated forewing appearance. Forewing statistics: ♂ FWL: 6.3–7.6 mm (mean = 6.8, $n = 18$), AR = 3.03; ♀ FWL: 6.5–7.5 (mean = 7.1, $n = 4$), AR = 2.90.

Male genitalia (Figs. 29, 36): Uncus with medial line of division developed into a prominent indentation in some individuals, basal width ca. $2 \times$ height; socii fingerlike and moderately setose; vesica with 8–14 deciduous cornuti ($n = 6$); valva tapering from base to neck, with concave costal margin and moderately

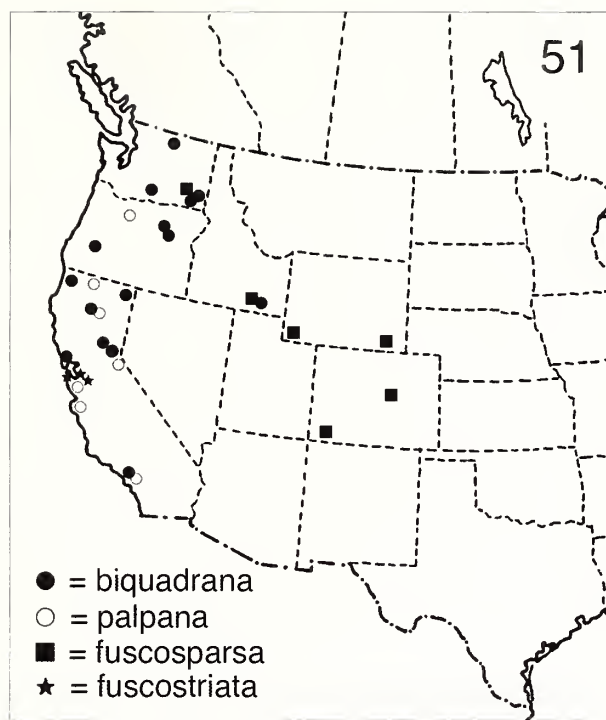


FIG. 51. Geographic distribution of *E. biquadrana*, *P. palpana*, *P. fuscosparsa*, and *P. fuscotriata*.

emarginated ventral margin; cucullus with apex semirectangular to rounded and with several stout setae distributed along ventral margin, the largest at distal end of neck. Female genitalia (Fig. 45): Papillae anales laterally facing, finely ridged transversely, with long ventrally curving setae along lateral margin; lamella postvaginalis roughly U-shaped, with a prominent medial indentation in the posterior margin and a shallow central trough from there to ostium; lateral sections of sterigma with long hairlike setae flanking central trough; posterior margin of sternum 7 with convex medial projection that fuses with sterigma to form a shallow lip at anterior margin of ostium; ductus bursae without sclerotization; corpus bursae with two signa, one small and tacklike, the other larger with winged apex.

Distribution and biology. I examined 26 specimens (21 ♂, 5 ♀), one from Jefferson Co., Oregon, and the rest from Monterey, San Bernardino, Shasta, Siskiyou, and Toulumne counties, California (Fig. 51). Capture dates range from early June to late July. No larval host has been reported.

Pelochrista gilligani, new species (Figs. 16, 30)

Diagnosis. This species is separated from its congeners by forewing color and maculation (Fig. 16), most conspicuously by the white polygonal line extending from subbasal fascia to ocellus. In size and male genitalia *gilligani* is closest to *palpana*, but the valva is more sharply constricted at the neck, the large ventral spine at the distal end of the neck is longer and more curved, and the projection supporting that spine tends to be larger.

Description. *Head:* Frons white to pale yellowish tan, vertex pale golden brown; labial palpi white with pale golden-brown sealing on lateral surface of second segment; antenna concolorous with vertex. *Thorax:* Dorsal surface concolorous with vertex, ventral surface white, legs pale yellowish tan with white tarsal annulations. *Forewing* (Fig. 16): ♂ FWL 6.6–7.0 mm (mean = 6.8, $n = 4$), AR = 3.25; costa weakly convex, apex acute, termen straight; dorsal surface light golden brown with white markings as follows: strongly expressed strigulae on distal one half of costa, a streak along the radius from base to distal end of discal cell, a narrow band along dorsum from base to subbasal farsia, a narrow band along termen, and a conspicuous, four segmented, polygonal line with proximal segment arising on dorsum and following distal margin of subbasal farsia to eubitus, next segment following eubitus half way to tornus, third segment bending toward apex and continuing to ocellus, and fourth segment following basal margin of ocellus to dorsum; ocellus pale golden brown, crossed longitudinally by two or three faint black dashes, bordered basally and distally by lustrous, transverse, ivory bars; termen lined with several rows of whitish scales with black medial marks; fringe pale golden brown. *Hindwing:* Dark gray with lighter fringe. *Male genitalia* (Fig. 30): Uncus a semicircular, dorsally setose lobe, basal width ca. $2 \times$ height; dorsolateral shoulders of tegumen well developed, socii fingerlike and moderately setose; gnathos bandlike; aedeagus bulbous anteriorly, narrow and tapering distally; vesica with 3 deciduous cornuti ($n = 2$); valva with costal margin concave, apex rounded, ventral margin moderately emarginated, with large, semitriangular, ventral projection at distal end of neck supporting a particularly long curved spine; cucullus with up to 3 spiniform setae at anal angle and with stout setae on medial surface. *Female genitalia:* Unknown.

Holotype. ♂, Utah, Sanpete Co., Ephraim Canyon Road, 9450 ft, 20 July 2006, T. M. & J. M. Gilligan, USNM. Type locality at 39°18'35" N, 111°27'36.7" W.

Paratypes. Same data as holotype (3 ♂, genitalia slides DJW 1911, 1912), TMG, DJW, USNM.

Etymology. This insect is named after Todd M. Gilligan, one of the collectors of the type series.

Distribution and biology. The four specimens in the type series were taken in a light trap placed in an aspen grove, elevation 9450 ft., a few miles east of Ephraim, Utah. Nothing is known about larval hosts.

Remarks. The number of stout spines on the distal margin of the cucullus is variable, both from specimen to specimen and from valva to valva of a single individual (Fig. 30).

Pelochrista fuscosparsa (Walsingham)

(Figs. 17–20, 31, 38, 46, 51)

Paedisca fuscosparsa Walsingham 1895: 507.

Eucosma fuscosparsa: Fernald [1903]: 460; Barnes and McDunnough 1917: 171; Heinrich 1923: 116; McDunnough 1939: 47.

Pelochrista fuscosparsa: Powell 1983: 35; Brown 2005: 479.

Types. Lectotype here designated (Fig. 38): ♂, [Larimer Co.], Loveland, Colorado, 5000 ft, Smith, July 1891, genitalia slide 11572, BMNH. Paralectotype: ♂, same data as lectotype, BMNH.

Descriptive Notes. This medium sized, grayish-brown moth is variable in forewing appearance. In some individuals

(Fig. 17) the color is nearly uniform, from pale tan to grayish brown, with only the slightest hint of darker markings; in others (Fig. 18) the ground color is sparsely overlaid with blackish-brown spots and speckles; and frequently (Figs. 19, 20) the areas between the veins are suffused with blackish-brown coloration, adding a longitudinally streaked effect. Dark marks in the median area sometimes (Fig. 18) appear to be remnants of a largely disintegrated median farsia, but otherwise there are no recognizable transverse markings. The ocellus is not expressed, and the fringe is uniformly pale tan. Hindwing color ranges from gray brown to dark gray brown, with fringe pale and contrasting. Forewing statistics: ♂ FWL: 7.9–13.3 mm (mean = 11.1, $n = 50$), AR = 3.22; ♀ FWL: 10.8–12.3 (mean = 11.6, $n = 3$), AR = 3.12.

Male genitalia (Figs. 31, 38): Uncus a strongly developed, semitriangular lobe with pronounced medial indentation, basal width ca. $1.5 \times$ height; dorsolateral shoulders of tegumen well developed, socii fingerlike and moderately setose; vesica with 12–27 deciduous cornuti ($n = 12$); valva with long, gradually narrowing neck; cucullus with apex rounded, anal angle moderately developed and supporting one stout spiniform seta, and distal margin with three or four more or less evenly distributed spines; margin of basal excavation with a raised clasperlike process. **Female genitalia** (Fig. 46): Papillae anales with posterior lobes ventrally facing, anterior lobes finely ridged transversely and ventrolaterally facing, lateral margins with long ventrally curving setae, anterior extremities and margins of anal opening with hook-tipped setae; lamella postvaginalis a broadly developed rectangular plate, width greater than $2 \times$ length, with rectangular medial indentation in posterior margin and long hairlike setae flanking indentation; lamella antevaginalis fusing with convex posterior margin of sternum 7; membrane between sterigma and ventral extremities of sternum 8 with long thin setae; ductus bursae short, broad, and encircled by narrow sclerotized ring at juncture with ductus seminalis; corpus bursae with some thickening of the membrane posterior to mid bursa and with two signa, one small and tack-like.

Distribution and biology. I examined 87 specimens (84 ♂, 3 ♀) from Colorado, Idaho, Washington, and Wyoming (Fig. 51). They document a flight period extending from late May to mid-August, but 85% of the capture dates fall between mid-June and the end of July. No larval host has been reported.

Pelochrista fuscotriata, new species

(Figs. 24, 32, 47, 51)

Diagnosis. This species has similarities with *mediotriata*, *fuscosparsa*, and *biquadrana*. In forewing pattern it most resembles *mediotriata* (Figs. 2, 3, 24), but worn specimens could be confused with dark phenotypes of *fuscosparsa* (Fig. 20). However, in *fuscotriata* the forewing fringe has a central band of pale coloration that is edged basally and distally by thin dark lines; in the other two species the fringe is unicolorous. Genitalic characters place *fuscotriata* closest to *fuscosparsa*. Males are separated by the shape of the uncus: broad and bulbous in *fuscotriata* (Fig. 32) vs. tapered and semitriangular in *fuscosparsa* (Fig. 31). Females of *fuscosparsa* have two well developed signa in the corpus bursae and a narrow sclerotized band that encircles the ductus bursae at the

junction with the ductus seminalis; in *fuscostriata* the signum on the ventral surface of the corpus bursae is reduced to a sclerotized linear scar, and the band on the ductus bursae is reduced to a small sclerotized patch. The shapes of the valva, sterigma, and papillae anales easily distinguish *fuscostriata* from *mediostriata* (Figs. 41, 47). The structure of the uncus in *fuscostriata* is very similar to that of *biquadrana*, but the two species are easily separated by forewing pattern (Figs. 24, 21), shape and armament of the cucullus (Figs. 32, 33), and structure of the lamella antevaginalis (Figs. 47, 48).

Description. *Head:* Frons pale tan to dark grayish brown, scales of vertex tan to brown medially, paler toward base and apex; labial palpi tan basally, shading to brown distally; antenna concolorous with vertex. *Thorax:* Dorsal surface concolorous with head; tegulae with pale tan apices; ventral surface tan; legs with ventral surfaces tan, dorsal surfaces brown; distal ends of tarsal segments ringed with paler scales. *Forewing* (Fig. 24): ♂ FWL 8.1–9.5 mm (mean = 8.9, $n = 3$), AR = 3.11; ♀ FWL 8.9–10.7 mm (mean = 9.8, $n = 2$), AR = 3.12; dorsal surface olive brown to blackish brown, with tan to whitish streaks along the veins; ocellus, fasciae, and costal strigulae not expressed; fringe with pale tan to whitish central band, bordered basally and distally by thin brownish-gray lines. *Hindwing:* Dark brownish gray; fringe lighter. *Male genitalia* (Fig. 32): Uncus a semicircular, medially divided, setose lobe, basal width ca. $3 \times$ height; dorsolateral shoulders of tegumen weakly developed; socii fingerlike and moderately setose; aedeagus long and tapering; vesica with 12 to 24 deciduous cornuti ($n = 4$); valva with costal margin weakly concave, apex evenly rounded, ventral margin weakly emarginated, and anal angle developed into a semitriangular projection supporting one large spine; margin of basal excavation with raised clasperlike process; cucullus with 2 to 4 spiniform setae along distal margin and with stout, densely distributed setae on medial surface. *Female genitalia* (Fig. 47): Papillae anales densely setose, with long ventrally curving setae along lateral margins; posterior lobes facing ventrally, anterior lobes very finely ridged transversely and facing ventrolaterally; lamella postvaginalis developed laterally into a shieldlike plate with rounded medial indentation of posterior margin; sternum 7 with semitriangular medial protrusion of posterior margin fused with sterigma; membrane between sterigma and ventral extremities of tergum 8 with numerous, long, hairlike setae; ductus bursae short, with small sclerotized patch at juncture with ductus seminalis; corpus bursae with two signa, one small and blade-like, the other reduced to a sclerotized linear scar on surface of membrane.

Holotype. ♂, California, San Mateo Co., Edgewood Park "A", J. A. Powell, 14 May 1991, genitalia slide DJW1968, EME.

Paratypes. CALIFORNIA: Same data as holotype (1 ♂, genitalia slide DJW1970; 1 ♀, genitalia slide DJW1971), USNM; Santa Clara Co., Kirby Cyn. Ridge NE of Morgan Hill, A. E. Launer, 21 May 1990 (1 ♂, genitalia slide JAP6365; 1 ♀, genitalia slide DJW1969), EME; San Benito Co., 15 mi. E of Gonzales, 19 May 1962, C. D. MacNeill (1 ♂, genitalia slide JAP1100), EME.

Etymology. The specific epithet is formed from the names *fuscosparsa* and *mediostriata*, the two congeners that this species most closely resembles.

Distribution and biology. Five of the six

specimens in the type series were collected diurnally in serpentine grassland habitat (J. A. Powell pers. comm.) in central California.

Eucosma biquadrana (Walsingham)
(Figs. 21, 22, 33, 39, 48, 51)

Paedisca biquadrana Walsingham 1879: 45.

Eucosma biquadrana: Fernald [1903]: 457, Barnes and McDunnough 1917: 170; Heinrich 1923: 129; McDunnough 1939: 47; Powell 1983: 35; Brown 2005: 316.

Eucosma palousana Kearfott 1907: 34; Barnes and McDunnough 1917: 170; Heinrich 1923: 130, Fig. 222; McDunnough 1939: 47, **new synonymy**.

Pelochrista palousana: Powell 1983: 35; Brown 2005: 480.

Eucosma tahoensis Heinrich 1923: 112, Fig. 230; McDunnough 1939: 47, **new synonymy**.

Eucosma tahoensis subditiva Heinrich 1929: 9.

Pelochrista tahoensis: Powell 1983: 35; Brown 2005: 481.

Discussion. The lectotype of *palousana* and the holotype of *tahoensis* are in rather poor condition, but in each specimen what can be seen of the forewing pattern is consistent with the markings of *biquadrana*. I compared the genitalia slides prepared by Heinrich for the two types with Obraztsov's slide for the *biquadrana* lectotype and found no significant differences. These observations are the basis for the proposed synonymies. Heinrich (1929) proposed the name *E. tahoensis subditiva* for what he considered to be a large variety of *tahoensis*, but there are numerous specimens of intermediate size, which render that distinction untenable, a conclusion previously reached by Powell (1983).

Walsingham (1879) reported two syntypes for *biquadrana*, the lectotype and paralectotype mentioned below, but his collection contained additional specimens from the type locality bearing labels such as "PAEDISCA BIQUADRANA Wlsm, ♂ PARATYE 4/7." This suggests that the original series consisted of the "Type" and at least 7 "paratypes." When Obraztsov examined the syntypes, he concluded that three of these additional specimens, Wlsm. Nos. 91892–91894, were not conspecific with the lectotype, and he placed on them labels with the inscription "not a paratype, N. Obraztsov det. 195_." I examined the lectotype as well as specimens 91893 and 91894 and could find no basis for treating the three as more than one species. Specimen 91894 is considerably smaller than the other two but is not substantially different in forewing appearance or genitalic structure. The size differences

are similar to those observed by Heinrich (1929) in separating *E. tahoensis subditiva* from *E. tahoensis*.

In the description of *palousana*, Kearfott (1907) mentioned 10 syntypes, 5 from Pullman, Washington, dated 11 July, 10 August, and 18 September, and 5 from Los Angeles, California, dated August and October. Heinrich (1923) pointed out that the California specimens are *Sonia filiana* Busck, and he stated that the "Type" of *palousana* is a male in the AMNH from Pullman, Washington. Klots (1942) reported three male syntypes in the AMNH: a lectotype from Pullman, labeled "*Eucosma palousana* K. Type CH 1921," and two paralectotypes [*S. filiana*] from Los Angeles. Under these circumstances, I think Heinrich did designate a particular specimen to be the name bearer, and consequently the lectotype selection is properly attributed to him. It appears that Kearfott (1907) misreported one or more of the capture dates of the syntypes, since the date on the lectotype (14 Aug 1898) does not agree with any of those mentioned in the description. In addition to the three AMNH specimens, I examined three syntypes at the USNM (1 ♂, 1 ♀ from Pullman; 1 ♂ from Los Angeles) bearing Kearfott's handwritten "Cotype" labels. Heinrich (1923) considered the female from Pullman to be conspecific with the lectotype, but it is not. Both of the USNM specimens from Pullman are representatives of an undescribed species of *Eucosma* in the *E. pulveratana* (Walsingham) species group. Finally, I examined one female specimen of *S. filiana* in the LACM which I think could be part of the *palousana* type series. It does not have a Kearfott determination label, but the date and locality labels are identical to one of the syntypes in the AMNH.

Types. *Paedisca biquadrana*. Lectotype here designated (Figs. 21, 39): ♂, Pit River, Shasta Co., California, 21–26 July 1871, Walsingham, No. 91890, genitalia slide 11517, BMNH. Paralectotype: ♂, same capture data as lectotype, abdomen missing, Wlsm. No. 91891, BMNH. *Eucosma palousana*. Lectotype designated by Heinrich (1923, Fig. 33): ♂, Pullman, [Whitman Co.], Washington, 14 August 1898, C. V. Piper, genitalia slide CH 20 Apr 1921, AMNH. *Eucosma tahoensis*. Holotype: ♂, Deer Park Springs, Lake Tahoe, California, 8–15 July, genitalia slide 72829, USNM. Paratypes: Deer Park Springs, Lake Tahoe, California, 1–7 July (1 ♂, AMNH; 1 ♂, USNM).

Descriptive Notes. The *biquadrana* forewing pattern (Figs. 21, 22) consists of a partially expressed subbasal fascia extending from dorsum to radius, a conspicuous pretornal patch on the dorsum that abuts the basal margin of the ocellus, and a well defined postmedian band extending from costa to termen and bordering the anterior and distal margins of the ocellus. The orientation of the subbasal fascia varies from oblique (Fig. 22) to nearly perpendicular to the dorsal margin (Fig. 21). There is some variation in the amount of contrast between the whitish ground color and the dark brown markings, which is due largely to differences in the intensity of the brown irrorations and gray suffusion in the interfascial areas. The ocellus is bordered basally and distally by lustrous white transverse bars which often

are suffused with pale pinkish-brown. Forewing statistics: ♂ FWL: 7.2–12.2 mm (mean = 10.2, n = 40), AR = 3.02; ♀ FWL: 8.2–11.2 (mean = 9.2, n = 7), AR = 2.89.

Male genitalia (Figs. 33, 39): Uncus well developed, height nearly equal to basal width, divided medially into two, laterally setose, bulbous lobes; socii long, pendulous, and moderately setose; aedeagus long and narrow; vesica with up to 7 deciduous cornuti; valva with costal margin concave, apex evenly rounded, distal margin convex, anal angle weakly developed, and neck long and narrow (width less than 0.5 × width of valval base); cucullus with long spine at anal angle and three or four similar spines evenly distributed along distal margin; margin of basal opening with weakly developed medial ridge. **Female genitalia** (Fig. 48): Papillae anales with posterior lobes ventrally facing, anterior lobes finely ridged transversely and ventrolaterally facing, lateral margins densely covered with long ventrally curving setae, and medial margins lined with hook-tipped setae; lamella postvaginalis with lateral semitriangular projections, acute posterolateral vertices, and a shallow trough extending from medial indentation of posterior margin to ostium; posterior margin of sternum 7 weakly concave and not closely approximate to sterigma; ductus bursae with weakly sclerotized patch opposite juncture with ductus seminalis; corpus bursae with two signa, one stubby and conelike, the other considerably smaller and tacklike; membrane in vicinity of juncture with ductus bursae variably wrinkled and thickened.

Distribution and biology. I examined 53 specimens (46 ♂, 7 ♀) from California, Idaho, Oregon, and Washington (Fig. 51). Capture dates range from late June to mid-August, but nearly all the records are from July. No larval host has been reported.

Eucosma shastana (Walsingham)
(Figs. 23, 40, 49)

Paedisca shastana Walsingham 1879: 46.

Eucosma shastana: Fernald [1903]: 457; Barnes and McDunnough 1917: 171; Heinrich 1929: 9, Fig. 10; McDunnough 1939: 47; Powell 1983: 34; Brown 2005: 327.

Discussion. This species is very poorly represented in collections; I was able to locate only two specimens besides the syntypes. One, in the USNM, is an exemplar given to Fernald by Walsingham. It was probably captured at the type locality, but there are no collection data on the pin (J.W. Brown pers. comm.). The other is a female in the AMNH from Mono Co., California. I examined the lectotype and the female in the AMNH; the following comments are based on those two specimens.

In his 1923 monograph, Heinrich confused *shastana* with *tahoensis* and included under the former name an illustration (Heinrich, 1923, Fig. 221) of the male genitalia of the latter species. He later (1929) corrected the error after receiving the Walsingham specimen of *shastana* from the Fernald collection.

Types. Lectotype here designated (Figs. 23, 40): ♂, Mt. Shasta, Siskiyou Co., California, 2 Aug.–1 Sept. 1871, Walsingham 91895, genitalia slide 11516, BMNH. Paralectotype: ♀, same data as lectotype, genitalia slide 11534, BMNH.

Descriptive Notes. The forewing pattern is very similar to that of *biquadrana* (Figs. 21–23), but the pretornal patch is broader, the postmedian band connects to the apical spot, and the overall appearance is more reddish brown than brown. The specimens examined had forewing lengths of 12.8 mm (♂) and 13.7 mm (♀), suggesting that this species is somewhat larger than *biquadrana*, which has a mean FWL of approximately 9.7 mm.

Male genitalia (Fig. 40): Uncus a rounded, dorsally setose lobe; dorsolateral shoulders of tegumen well developed; socii fingerlike, vesica with 14 deciduous cornuti ($n = 1$); valva with dorsal margin concave, apex strongly produced and evenly rounded, distal margin convex, anal angle weakly developed and evenly rounded; cucullus with medial surface densely covered with fine setae and with distal margin lacking stout setae. **Female genitalia** (Fig. 49): Papillae anales laterally facing and finely ridged transversely, with lateral margins lined with long ventrally curving setae and medial margins near anal opening lacking hook-tipped setae; sterigma ringlike, with acute posterolateral projections; membrane between sterigma and ventral extremities of sternum 8 with numerous, long, hairlike setae; ductus bursae with small sclerotized patch at juncture with ductus seminalis; corpus bursae with two signa of nearly equal size.

Distribution and biology. Of the four specimens mentioned above, two were collected at Mt. Shasta in northern California and one at Casa Diablo Hot Springs, a few miles southeast of Mammoth Lakes, California. All appear to have been captured in August. No larval host has been reported.

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STEPHEN ROGERS STEINHAUSER

(1921–2007)

Stephen Rogers Steinhauser (Fig. 1), a life member of the Lepidopterists' Society, died on August 11, 2007 at the Sarasota Memorial Hospital at the age of 86. He was an avid collector of butterflies and moths from childhood, especially in the neotropics, where he also studied the life histories of several species. Steve was a Research Associate of the Allyn Museum of Entomology and the McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida and published numerous taxonomic papers on the HesperIIDae and Nymphalidae. He is survived by his wife of 13 years, Josephine F. Steinhauser, his daughter, Nancy Murray, and son, Peter, West Hartford, Connecticut, a stepson Larry Lloyd, Houston, Texas, a stepdaughter, Mary Lloyd, Mesa, Colorado, two grandchildren and four step grandchildren.

Steve Steinhauser enjoyed a very rich and colorful life. Born on May 15, 1921 in Newburgh, N. Y., he was the son of Harry H. Steinhauser and Muriel W. Rogers. He lived in Weston and Westport, Connecticut, Madison, New York as well as New York City. He had one brother, Harry H. Steinhauser, Jr. His father was a civil engineer, and as children, they spent some time with their father in Guyama and Arecibo, Puerto Rico while he was building a dam. Steve graduated at the top of his class from George Washington High School in New York City. Both Steve and his brother attended Princeton University, with Harry graduating in 1941 and Steve in 1942 with a degree in geological engineering. Harry Steinhauser, Jr. went on to receive a doctorate in mechanical engineering from the University of Michigan, was a professor at MIT, and then became the Dean of Mechanical Engineering at the University of New Haven, Connecticut.

Steve had originally planned to enter the Navy V-7 Program in May, 1942 and had gone to New York for his physical. He was asked to return the following Monday to complete the exam. During the intervening weekend, he collided with another student during a softball game, suffered a concussion, broke his jaw, and one big toe. He contacted the Navy during the following week and was told to come back to New York once he could open his mouth again. This gave Steve an opportunity to reconsider his original plan, and he decided to take a position in essential industry as an

assistant mining engineer with Anaconda Copper Mining Co., in Butte, Montana, where he worked from August 1942 to May 1944. In the spring of 1944, the age limit for industrial deferments was raised to 26, and Steve found himself eligible for the draft once again. He reapplied to the Navy and was awaiting his commission. However, the draft board in Connecticut told him to report for induction into the Army, and he was sent to Fort Devens, Massachusetts. Two days later his Navy commission came through, and he spent the next five days trying to make the transfer. He was eventually sworn into the Navy by an Army colonel and following that induction, he was discharged from the Army. These kinds of interesting and out of the ordinary experiences followed Steve throughout his service in the South Pacific. He was finally discharged in June, 1946. In retrospect, we believe that these experiences had a profound effect on his outlook on life and made him a survivor in any situation.

Following the war, he worked as a carpenter building houses and other jobs in Weston, Connecticut. Steve then had an opportunity to rejoin the Anaconda Copper Mining Co. as a mining engineer in October, 1948, continuing until June, 1952. He later was employed as a geologist with the U. S. Atomic Energy Commission (June, 1952–November, 1959) and was stationed in Richfield, Utah, Karnes City and Austin, Texas, and Grand Junction, Colorado. Steve met his wife, Levona, while working for the AEC in Grand Junction. In November, 1959, Steve joined the United Nations

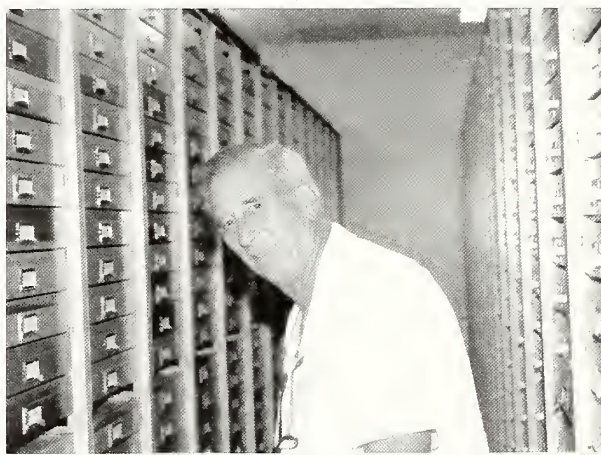


FIG. 1. Steve Steinhauser at work on HesperIIDae in the Allyn Museum collections in 2002.

Development Programme (UNDP) and served as an economic geologist on various projects for more than 20 years, including stops in Rangoon, Burma, now Myanmar, (1959–1962), the Bawdwin Mine, Northern Shan States, Burma (1962–1964), Ovalle, Chile (1964–1966), Pan Cordillero, Mendoza, Argentina (1966), Santiago, Chile (1966–1967), San Salvador, El Salvador (1967–1972), and Cali, Colombia (1973–1976). Steve was the project manager for the last two stations (1967–1976). He ultimately did one more contract with the UNDP as a Project Director, at Camp Jaguar, New River Area in southern Guyana near the Brazilian border in 1980. As a project director, Steve was noted for his relaxed managerial style that fostered an atmosphere in which people really enjoyed doing what they were paid to do (pers. comm. L. Lloyd and I. Naylor). Given the amount of bureaucracy involved with each different country, they managed to accomplish much while enjoying each country and its associated culture to the fullest.

There were many adventures in Burma, including the fact that they were in Rangoon when General Ne Win completed his coup d'état in 1962, and the family experienced the nationalization of Rangoon which occurred thereafter. On many occasions, Steve was accompanied into the field with government escorts due to insurgents. There were other memorable moments concerning the cultural differences while working in a foreign country. For example, there had been some problems with the motor on the UN jeep at the Bawdwin mine, Burma. One afternoon, Steve arrived home to find the entire motor removed from the vehicle and various parts of the motor carefully taken apart and neatly lined up by one of his assistants. Steve was assured that the motor would be fixed and would be in working order shortly. Surprisingly, the assistant was able to fix the shims on the pistons, and the jeep worked very well for the rest of their stay. On another occasion while celebrating Thanksgiving at the Bawdwin mine, the meal consisted of buttered rice and spam. His stepson, Larry Lloyd, also remembers Steve and him crawling through an underground mine with just enough room to squeeze through to find the miners sitting next to canaries in cages. The workers at some of these remote mines were paid with opium. Such experiences put everything about life in perspective.

Steve spent a number of years at each location and his family often accompanied him. When he went into the field to do geological exploration, this not only afforded him some time to look for interesting mineral deposits but allowed him an opportunity to collect unusual butterflies, so his butterfly net and associated

equipment always went along. Occasionally he was on horseback or on an elephant, depending on the country, holding a mining pick in one hand and a butterfly net in the other. The roads in a number of these remote areas were not the best, and sometimes Steve and his crew spent several hours, indeed some days, along the side of the road stranded due to torrential rains and mudslides. Steve always made the most of any free time by also searching for larvae. It is rather unusual that as part of his resume, Steve listed butterfly collecting in Papua, New Guinea (June 1964) and also during some vacation time in El Salvador (Dec., 1972–May, 1973). The remarkable aspect about the development of his collection was that Steve did not become interested in the Hesperiidæ until long after his travels to Myanmar and that side trip to New Guinea. He certainly made up for lost time later.

We first met Steve and his then wife, Levona, at the 1972 Annual Meeting of the Lepidopterists' Society at Louisville, Kentucky. During the Thursday evening mixer at the home of Charlie and Betty Covell, we had an opportunity to speak with them at length about the possibility of ultimately retiring to Sarasota, Florida. In 1973, we hosted the Lepidopterists' Society meetings at the Allyn Museum of Entomology, and Steve and Levona made the trip from El Salvador in a Volkswagon microbus. Just prior to those meetings, Arthur Allyn, our Director, purchased their collection for the Museum. Due to their nomadic lifestyle, this was for the most part a basic synoptic collection with the bulk of the specimens still in papers. However, there was much material (including moths) from Burma, Argentina and elsewhere that now, with other collections, provides a historical time line for species biodiversity in those countries. In addition, there were also some very uncommon butterflies, such as a series of *Hermathena oweni* (Riodinidae) and *Argyrophorus argentius* (Satyrinae), but most importantly, there were also long series of skippers from various locations, including a number of reared specimens.

During this period, Steve and Levona began to look around the Sarasota area for a potential place to retire. They ultimately found 10 acres north of the city along a then dirt road (County Line Road, now University Parkway) and were finally able to move there in 1977. They expanded the small house to 5,000 sq. ft., based on Steve's own architectural plans and did a lot of work themselves, including finishing the interior. He was an expert carpenter and hand crafted the kitchen cabinets. Steve added some unusual features to the house, such as the wood spiral staircase from the kitchen to the upstairs areas. He also made one of the most unusual



FIG. 2. The curatorial-phylogenetic "chorus line" at the Annual Meetings, at the University of New Mexico, Albuquerque. From left to right, Phillip Ackery, Dick Vane-Wright (both of BMNH), Steve Steinhauser and Lee Miller in 1989.

coffee tables, which was a cross section (6 ft. x 10" thick) through a large tree obtained in Argentina. He was also a skilled woodcarver and craftsman, who built his own butterfly storage cases and beautiful cabinets.

Steve had a broad variety of interests. He enjoyed bowling and was active with the leagues in El Salvador, Colombia, and Sarasota for a number of years. He was a jazz enthusiast and had hundreds of recordings in his archival library. In addition, Steve enjoyed cooking and was an avid reader. He liked to garden and enjoyed growing and cooking all kinds of hot and regular peppers. He developed an inordinate number of recipes for stuffed green peppers and could have written a cookbook on the subject. Steve occasionally took some of the semester courses offered at various sites in Sarasota with topics that ranged from politics and economics to energy reduction (including battery powered cars), long before this current wave of discussion on sustainability.

Capturing the essence of Steve is rather difficult. As a colleague at the Museum, he was exceedingly serious about examining various morphological characters and puzzling out some of the close affinities of hesperiid species. During his work day, there was always some

new joke or observation on the world at large that brought a smile to your face or a new outlook on life. Dr. Gavin Naylor, son of Ian Naylor, one of the project team in El Salvador and now an Associate Professor of Biological Science at Florida State University provided a few of these. Steve pointed out that when anyone called and left a message on the telephone answering machine stating, "Please call back. It's important," it invariably meant that it was important for THEM, not you!

An inveterate story, punster and joke teller, Steve went for more than a week on a fishing trip and never repeated a single joke much to the amazement of all present. He was a fun loving guy and traveling with him was always an experience. We drove to Laramie, Wyoming, for the annual meetings in 1982, and Steve regaled us with stories and jokes the entire way. Cliff Ferris, the chair of the meetings, had organized everything exceedingly well. However, when we got to the Sunday morning session, there was coffee and tea, but the donuts were limited. Steinhauser remembered the jalapeno cheese bread that we had purchased the day before for a taste test. Steve thought that it was far too mild, but it became part of the Sunday morning

break menu and was consumed without any complaints. Then there were the meetings in Albuquerque, New Mexico, when Phillip Ackery and Dick Vane-Wright both won the Karl Jordan Medal for their work on the *Biology of Lepidoptera* and especially for their volume on the *Milkweed Butterflies*. One evening, we decided to go out to dinner to one of the better restaurants that overlooked the city. This also included Karolis Bagdonas and that made six people in a mid-sized car that should only accommodate five. Steve piped up that this traveling group of troubadours should be known as the "Albaturkeys", and things went on from there. Following dinner, we went to put some books and backpacks in the trunk. The ever reserved Phil Ackery decided that he wanted a more relaxed ride back and jumped into the car trunk before anyone could say anything more. Once this camaraderie started, it continued through the end of the meeting and resulted in the phylogenetic photo (Fig. 2) the following day in the dormitory parking lot, with Phil, Dick, and Steve (the chorus line), and Lee, the outgroup. Lepidopterists are indeed unusual individuals, but we do have fun.

One of Steve's true passions was Lepidoptera, especially the Hesperiidae, and this included taxonomic and systematic in addition to life history studies. When he arrived in Sarasota, he just took a little time to learn how to complete expert genitalic dissections of both males and females. Although he began with just lateral views of male genitalia, these efforts were expanded to dorsal and ventral views. Consequently, he discovered a number of unique and different features. He also began to use female genitalia as part of his revisionary studies, including the development of the accessory glands as an important structure. He took great pride in the inked versions of his drawings, using a 000 pen to complete them. Later he became accomplished with various computer programs for illustrations and cladistic analyses.

Steve was a self starter and initially began to work as a volunteer in 1979 and later as a part-time staff member at the Allyn Museum, answering inquiries, identifying skippers and integrating these into the main collection. He devoted an inordinate amount of time working on Evans' J group skippers, especially the small dark genera and did untold number of genitalic dissections trying to match up males and females from the same locality. Gradually his studies expanded into some rather large revisionary studies on the Pyrginae. His dissections on the group and illustrations were meticulous, and he never tired of trying to help others to identify material. Thus far, he is author or co-author

of more than 23 published papers, including the description of more than 88 subspecies. A number of other papers will be published shortly.

Steve has been honored with four patronymial names in Lepidoptera:

Narcosinus steinhauseri G. T. Austin 1996. Journal of the Lepidopterists' Society, 50: 54–60.

Dalla steinhauseri H. A. Freeman. 1991. Tropical Lepidoptera, 2(1): 65–67

Dismorphia crisia steinhauseri 1984. J. de la Maza & R. G. de la Maza. Revista Sociedad Mexicana de Lepidopterología, 9(1): 3–12.

Cyllopsis steinhauserorum L. D. Miller. 1974. Bulletin of the Allyn Museum, 20: 26–29.

Stephen R. Steinhauser was indeed a renaissance man in every sense of the word, and his life revolved around a lot of things, but primarily his alma mater, Princeton University, and Lepidoptera. As his wife, Josie, remarked, "On one hand, he was a happy-go-lucky guy, but when it came to science, and especially, butterflies, he was very meticulous in his pursuits." He had a major impact on his children's lives by taking them into the field to discover nature whether it was fishing, looking for Inca artifacts, or watching male Atlas moths attracted to a newly emerged female at their house one night in Rangoon, Burma. He made a difference in a number of people's lives over the years by encouraging amateur collectors to complete dissections or just scan in a pencil genitalic sketch and finish it on the computer. Amateurs have contributed markedly to our knowledge of the Lepidoptera over the years, and Steve is a prime example of such major contributions. He instilled a sense of discovery and adventure for food, bugs, plants and/or anything else. Steve's sense of humor was legendary and despite his infirmities in later years, he continued to teach us how to deal with life. Steve was a scholar, a co-author, a friend, and a joyful person to be around whether you were the Keeper of the Entomology at the Natural History Museum, London, or the plumber, who came into to complete some repairs at the house. It is this human perspective that we will miss the most.

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- . 1974. Notes on neotropical Nymphalidae and Hesperiidae with descriptions of new species and subspecies and a new genus. Bulletin of the Allyn Museum 22: 1-38, 94 figs. (*Adelpha albifilum*, *Ridens crison howarthi*, *R. toddi*, *R. fieldi*, *Bolla salva*, *Erbietas sappho*, *Onespa* (new genus), *O. nubis*, *McIlana thecla*, *M. tamana*, *M. balsa freemani*, *Vaccra cervara*)
- . 1975. An annotated list of the Hesperiidae of El Salvador. Bulletin of the Allyn Museum 29: 1-34, 1 map.
- & L. D. MILLER. 1977. Three new species of *Adelpha* (Nymphalidae) from Mexico and Colombia. Bulletin of the Allyn Museum 46: 1-10, 22 figs. (*A. leona*, *A. escalantei*, *A. jacquelinac*)
- . 1981. A revision of the proteus group of the genus *Urbanus* Hubner (Lepidoptera: Hesperiidae). Bulletin of the Allyn Museum 62: 1-41, 61 figs. (*U. dubius*, *U. magnus*)
- . 1983. Notes on *Ridens* Evans, 1952 with description of a new species from Mexico. Bulletin of the Allyn Museum 79: 1-7, 6 figs. (*R. mercedis*)
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FORCIPOMYIA (MICROHELEA) FULIGINOSA (MEIGEN) (DIPTERA: CERATOPOGONIDAE), AN
ECTOPARASITE OF LARVAL *ANAEA TROGLODYTA FLORIDALIS* (NYMPHALIDAE)

The Florida leafwing, *Anaea troglodyta floridalis* F. Johnson and Comstock (Nymphalidae), occurs locally within the pine rocklands of southern Florida and the lower Florida Keys (Minno & Emmel 1993; Smith *et al* 1994). Hennessey and Habeck (1991) and Worth *et al* (1996) described many aspects of *A. t. floridalis* natural history. Salvato & Hennessey (2003) also discussed *A. t. floridalis* ecology and provided a review of known parasites and predators for the species. Although several larval parasites have been mentioned for *Anaea* Hübner (DeVries 1987) and similar genera (Muysshondt 1974a, 1974b; Caldas 1996) throughout tropical America, little has been reported for *A. t. floridalis* larvae.

On 19 January 2008 MHS and HLS observed a female biting midge (Diptera: Ceratopogonidae) attached to the cuticle of an early instar *A. t. floridalis* larva (Figure 1) in the Long Pine Key region of Everglades National Park (Miami-Dade County, Florida). After photographing the observation in the field, the midge and larva were collected together. The midge was encountered on the *A. t. floridalis* larva at 1200 h and it remained feeding and in the same position on the larva throughout collection and transport home (3 h). At approximately 2300 h on 19 January 2008 the midge detached itself from the larva, however, both midge and larva were maintained within the same

mesh-screened cage for an additional 24 h. After initial detachment, no further midge-larval interactions were observed.

The midge was preserved in 100% ethanol and sent to WLG who cleared it in phenol-alcohol, dissected and mounted it onto a microscope slide and identified it as *Forcipomyia (Microhelea) fuliginosa* (Meigen). *Forcipomyia (M.) fuliginosa* is a cosmopolitan ectoparasite that preys on a variety of insect groups, including Lepidoptera (Wirth 1956, 1972a; Lane 1984). In Florida, *Phocbis sennae* L. (Picridae) (Suzanne Koptur, pers. comm.) and *Erinnyis ello* L. (Sphingidae) (Knab 1914; Wirth 1956, 1972b; Borkent & Wirth 1997) larvae have been previously identified as hosts of *F. (M.) fuliginosa*. After identification, the *F. (M.) fuliginosa* specimen was deposited into the South Florida Collection Management Center at Everglades National Park.

The *A. t. floridalis* larva was maintained in a screen mesh cage and provided fresh food plants (*Croton linearis*, the only known hostplant for the species). MHS and HLS have successfully reared numerous *A. t. floridalis* larvae under these conditions over 11 years of research on this species. However the *A. t. floridalis* larva, which behaved lethargically in the field and laboratory, fed only minimally until dying at approximately 48 h after its discovery. In some instances, the role of *F. (M.) fuliginosa* as ectoparasites of Lepidopteron larvae is sub-lethal (Sevastopulo 1973; Young 1983). However, Wirth (1972) and Koptur (pers. comm.) have indicated that instances of larval death noted in the literature may be the result of *F. (M.) fuliginosa* vectoring microbes during feeding. Given the widespread distribution of *F. (M.) fuliginosa* in Florida (Wilkening *et al.* 1985; Hribar & Grogan 2005), the role of this ectoparasitic biting midge on the natural history of *A. t. floridalis* and other Lepidoptera requires further examination.

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FIG. 1. An early instar *Anaea troglodyta floridalis* larva being attacked by a female biting midge, *Forcipomyia (Microhelea) fuliginosa* on 19 January 2008 in Long Pine Key, Everglades National Park (Miami-Dade County, Florida) (Photo Credit: H. L. Salvato).

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